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Influence of Eastern Hemlock on Aquatic Biodiversity in Delaware Water Gap National Recreation Area



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EXECUTIVE SUMMARY

Craig Snyder

Eastern hemlock (*Tsuga canadensis*) occurs in cool, moist, hillside and ravine environments throughout the eastern United States (Harlow 1942). Hemlock stands and forests are valued as riparian and forest habitat (DeGraaf and Rudis 1986, DeGraaf et al. 1992) and as a commercial timber and horticultural species. Hemlock stands are also frequently targeted as desirable recreational areas on public lands because of their distinctive aesthetic, recreational, and ecological qualities (Evans 1995).

In the last two decades, substantial declines in eastern hemlock have been observed throughout its range, resulting in extensive Federal and state concern (Lapin 1994, Evans 1995). Widespread hemlock defoliation and mortality has largely been attributed to the hemlock woolly adelgid (*Adelges tsugae*, HWA), an exotic aphid-like insect that is native to Japan (McClure 1990). Resource managers expect the adelgid to continue to spread and consequently the entire hemlock forest ecosystem may be threatened. Recent studies suggest that hemlock regeneration following infestation is largely absent because smaller trees are at least as vulnerable to the pest as larger ones, and recruitment patterns in affected stands in Connecticut suggest hemlock forests will be replaced by mixed hardwood forests (Orwig and Foster 1998). A similar lack of regeneration occurred during the mid-Holocene when hemlock forests throughout North America went through a period of rapid, pathogen-induced decline (Fuller 1998). During that bottleneck, it took about 2000 years for hemlock to recover from the decline. Thus, there is a reasonable likelihood that forest stands killed by HWA will be lost indefinitely.

The impact of the removal of this important climax forest species on the ecology of Appalachian forests is poorly understood, but has the potential for significant disturbance to biotic communities by changing the energy inputs, micro-climatic environments, and physical habitat structure available to other vegetation, bird, mammal, and aquatic communities. Consequently, there is an urgent need to characterize the contribution of hemlock forests to biological diversity and functional stability in large, forested landscapes, and to identify contributing or ameliorating environmental conditions (both abiotic and biotic) that influence hemlock decline. Such information could provide the basis for future restoration strategies and serve as indicators of potential risk to hemlock forests not yet infested.

At the request of the National Park Service, the Leetown Science Center (LSC) conducted a comparative study designed to determine the potential long-term consequences to aquatic invertebrate and fish communities due to hemlock forest decline. We began by conducting a landscape analysis of the Park using Geographic Information Systems (GIS), and used the results to select 14 hemlock and hardwood site-pairs that were similar in topography (i.e., slope, terrain shape, aspect, light levels) and stream size but differed in forest composition (hemlock vs mixed hardwood). This paired watershed approach provided a powerful means to discern the influence of hemlock forests on stream communities, and provided an aquatic perspective on what we

stand to lose in terms of biological diversity, should hemlock forests die.

We found aquatic invertebrate diversity to be strongly influenced by forest composition. Specifically, streams draining hemlock forests supported on average 37% more taxa than streams draining hardwood forests, though the significance and magnitude of the forest effect depended on stream type (as determined by terrain characteristics and stream size). In addition, 10% of invertebrate taxa encountered in DEWA occurred significantly more often in streams draining hemlock. In contrast, total invertebrate densities and the probability of occurrence of rare taxa were higher in streams draining hardwood forests. Trophic composition also differed between forest types with hemlock-dominated watersheds supporting more predators and fewer scrapers (algivores). This suggests that stream ecosystem function (e.g., rates of nutrient and carbon processing) might also differ between forest types.

Our inferences regarding forest effects on fish communities are less clear because a significant number of selected stream sites dried up during the summer of 1997 compromising sampling and statistical analyses. Nevertheless, based on more descriptive comparisons, it appeared that both fish diversity and abundance were higher in streams draining hardwood forests. In contrast, there was relatively convincing evidence that the occurrence and abundance of brook trout (*Salvelinus fontinalis*), an important fishery in DEWA, were higher in streams draining hemlock. For example, brook trout were nearly three times more likely to occur in streams draining hemlock forests. As with aquatic invertebrates, streams draining hemlock supported more predator species (largely due to more trout).

Analysis of instream habitat data indicated no single habitat variable directly correlated with aquatic invertebrate diversity or brook trout abundance differences observed between forest types. However, we found forest composition had a significant, concomitant influence on several habitat variables, each of which could have contributed to differences in aquatic community structure. Specifically, habitat diversity was higher, total nitrite concentrations lower, and temperature and flow patterns more stable in streams draining hemlock than in those draining mixed hardwood forests. Although the greater variety of microhabitat types and lower total nitrite concentrations observed in hemlock-drained streams may have contributed to aquatic community differences, we believe that hemlock mediated increases in thermal and hydrologic stability were probably most important in explaining higher invertebrate diversity and brook trout abundances.

In summary, we predict a significant reduction in aquatic invertebrate diversity and brook trout abundance in DEWA should hemlock forests succumb to HWA. From a broader perspective, lower invertebrate diversities in these small streams would likely result in measurable reductions in diversity park-wide, and may cascade to other assemblages, both aquatic and terrestrial. Furthermore, the observed hemlock effects on stream conditions may have a significant influence in other parts of the drainage basin as well. For example, hemlock-mediated increases in thermal and hydrologic stability may affect habitat in the Delaware River. Survival and productivity of Delaware River fishes, particularly trout and shad, may be limited by the relative severity of

summer, base-flow conditions. Stable discharges of cooler water from hemlock-dominated tributaries may provide refugia for some species during these summer extremes.

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Chapter 1: A landscape-based sampling design to assess biodiversity losses from eastern hemlock decline

John A. Young, David R. Smith, Craig D. Snyder and David P. Lemarie

INTRODUCTION

In this chapter we describe the development and implementation of a landscape-based, stratified-pair sampling design to analyze differences in aquatic biodiversity between streams draining eastern hemlock (*Tsuga canadensis*) forest stands and those draining hardwood forest stands in Delaware Water Gap National Recreation Area (DEWA). We used geographic information systems (GIS) to assess and summarize landscape variation by forest stand, and statistical analysis to exploit this landscape information by stratifying terrain conditions and pairing similarly structured hemlock and hardwood streams prior to sampling. We found that the stratified pair design effectively reduced terrain influences and highlighted community differences due to vegetation. Use of this methodology allowed us to sample effectively a wide range of conditions while ensuring a balanced design that controlled for landscape variability.

Landscape assessments using GIS techniques are increasingly being used to characterize habitats for wildlife and growing environments for plants. These computerized mapping systems allow for the integration of large amounts of spatial and attribute data over broad areas, providing land managers and scientists with vast amounts of data detailing the variation of environmental parameters such as topography, soils, water resources, and geology (Stow 1993, Burrough 1986). Landscape information can be combined in various ways within a GIS to produce ecologically relevant groupings that can be analyzed for relationships to plant growth, species distribution, or wildlife-habitat interactions (Bailey 1996, Davis et al. 1990, Band 1989, Davis and Dozier 1988). Of particular application to fisheries and wildlife studies are techniques for classifying landforms from digital representations of topography that allow an assessment of geomorphologic influences on terrestrial and aquatic habitats (Błaszczynski 1997, Davis and Goetz 1990, Skidmore 1990, McNab 1989, Jenson and Dominque 1988).

Maps of landscape factors can also be exploited in sampling designs to optimize placement of field samples that capture the range of natural variation while minimizing logistical requirements (eg. time and personnel) (Haila and Margules 1996, Gillison and Brewer 1985). When combined with appropriate statistical designs, optimized sample placement using GIS can help to reduce sources of large-scale variation that can confound attempts to determine differences between field samples collected at random locations (Bourgeron et al. 1994, Austin and Heyligers 1989). Uncontrolled spatial sampling schemes may introduce confounding sources of variation (e.g. error) into comparative analyses by selecting sites in different geology, climate, topography, or degree of impact by other types of disturbance. Block, or stratified designs can help to control for sample site variation, as long as relevant environmental information is used to define strata (Bailey 1993). Additionally, pairs of sites within strata can be selected where variance among environmental

variables is minimized except for the effect under consideration. This stratified- pair design can help to isolate the effect under consideration and produce stronger comparisons and lead to more relevant inferences.

SETTING

DEWA is located in northeastern Pennsylvania and western New Jersey (Figure 1-1, Inset A). The park encompasses approximately 27,742 hectares of forested hills, ravines, and bottom lands straddling the Delaware River. The park was initially established in 1965 as part of the controversial Tocks Island dam project. While land acquisition and housing relocation was completed in the 1970's, the dam was never constructed and was officially de-commissioned in 1992. Today, abandoned roads and the foundations of many former residences can be found throughout the park. The area surrounding the park is still heavily settled and is a popular resort destination.

Approximately 21,885 hectares of DEWA is forested, of that total approximately 18,575 ha is deciduous forest, 1,295 hectares is evergreen forest, and 2,015 hectares is mixed evergreen-deciduous forest (Myers and Irish 1981). The dominant hardwood species are red oak (*Quercus rubra*), followed by sugar maple (*Acer saccharum*), chestnut oak (*Quercus prinus*), red maple (*Acer rubrum*), and sweet birch (*Betula lenta*). Dominant evergreens are white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*) and red cedar (*Juniperus virginiana*). Although eastern hemlock occurs in nearly pure stands, it also occurs as a significant understory species due to its shade tolerance. Altogether, eastern hemlock occurs as a primary, secondary, or tertiary forest component in approximately 1,130 forested hectares within DEWA (Myers and Irish 1981). Because the focus of this study was eastern hemlock, we defined an eastern hemlock stand as comprising either the primary, secondary, or tertiary forest component.

The physical setting of DEWA is varied with terraced benches and ravines to the east, significant river bottom habitats surrounding the Delaware River, and steeply sloping ridge habitats to the west. Minimum elevation is approximately 84 meters and maximum elevation is approximately 490 meters. Approximately 60 kilometers of the Delaware River flow through the park. Additionally the park has some 87 kilometers of 1st order streams, 32 kilometers of 2nd order streams, and 60 kilometers of 3rd or higher order streams, many of which originate outside the park.

METHODS

Map analysis

We used GIS to develop and manage landscape data and to create landscape-based strata used for the stratified-pair design. We developed sampling strata that captured environmental factors (vegetation, terrain, and stream size) deemed to have importance in structuring aquatic communities. Since the basis for our aquatic community comparisons would be vegetation

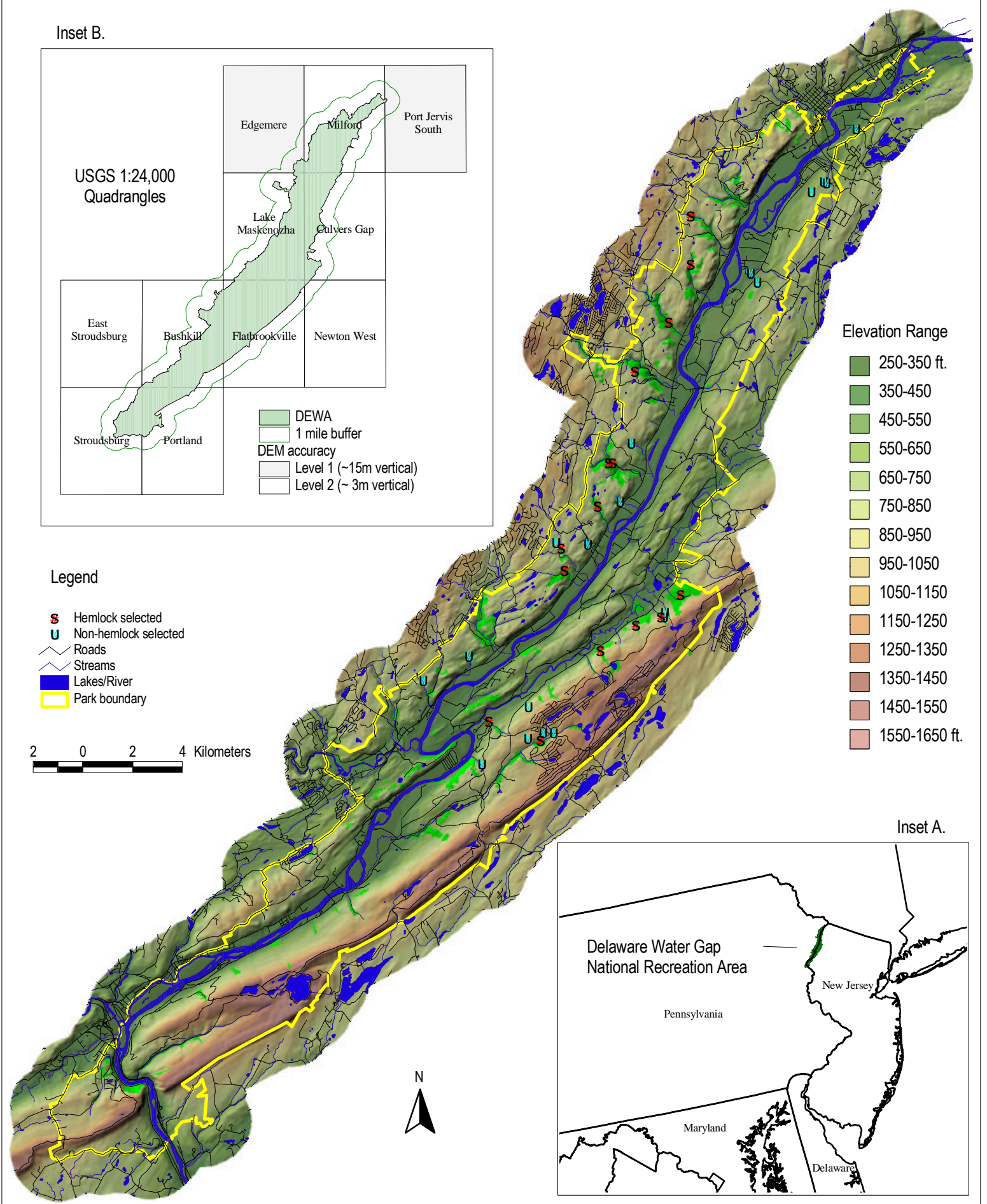


Figure 1-1. Delaware Water Gap National Recreation Area (DEWA) depicting terrain (as shaded elevation), location of hemlock stands (bright green), road systems, and stream drainages. USGS 1:24,000 quadrangles used as basis for modeling are shown in Inset A. Location of Delaware Water Gap NRA depicted in Inset B.

differences (i.e. hemlock versus hardwood forests), we used a digital vegetation map to classify land cover types and separate eastern hemlock forests from other forest types. Terrain has an important role in structuring aquatic communities by regulating energy and allochthonous inputs such as temperature and moisture patterns, incident light, and delivery of soil and plant materials to streams (Frissell et al. 1986, Cummins 1992). We characterized terrain by deriving measures of elevation, slope, aspect, shape, and shade from a digital terrain model. Lastly, because stream size and position in the drainage network strongly influence aquatic community structure (Minshall et al. 1985, Osborne and Wiley 1992), we characterized stream size (order) and length using a digital stream map.

DEWA personnel provided digital GIS coverages of vegetation, roads, streams, and boundaries. Vegetation was mapped from 1:12,000 aerial photographs by DEWA personnel in the early 1980's (Myers and Irish 1981). Vegetation is grouped into "stands" or polygons of similarly structured plant composition on this map; each stand is coded with cover type, species composition, and crown closure. Because the vegetation map contained non-forest vegetation components (eg. grasses, herbaceous plants, agriculture, etc.) as well as forest components, we created a new file containing only forest polygons to use in subsequent analysis. In addition, we divided polygon boundaries for forest stands into separate files for hemlock and non-hemlock forests. The vegetation map defined primary, secondary, and tertiary vegetation composition for each stand, reflecting the dominance by canopy area in each species. Because effects on hemlock were of interest, we placed stands with hemlock defined as either the primary, secondary, or tertiary component into a hemlock stand file (N=142 stands). All other forest stands were placed into a separate non-hemlock forest stand file (N=2145).

After initial polygon selection, we converted all GIS maps to a grid representation where geographic space is divided into a matrix of equal size cells of a given ground distance. In this grid or "raster" representation, each cell is tagged with an attribute (eg. elevation, forest type, etc.), and a stand is represented as a collection of cells with identical attributes. We used a cell size of 30 meters ground distance for compatibility with existing digital elevation maps used for terrain modeling. We conducted subsequent analyses using both the grid and polygon representations of forest stands (and other GIS files); the map representation used depended on the requirements of a particular analysis task and the tools available in Arc/Info (ESRI, Inc.: Redlands, CA).

We merged 10 U.S. Geological Survey 1:24,000 Digital Elevation Model (DEM) files together using Arc/Info to form a seamless elevation map for DEWA. In these files, elevations are recorded at regular intervals (as meters above sea level) at points separated by 30 meters ground distance. Conversion of these files into a GIS layer creates a regular grid of elevations with one elevation value per cell. Vertical accuracy of these files is reported to be " 3 meters for 8 of the 10 DEM files and " 15 meters for 2 of the DEM files (USGS, 1995). Differences in accuracy reflect mapping methodology used to record elevations from source materials (USGS, 1995). Due to the orientation of the park boundary in relation to the DEM files, the lower accuracy files affected only small portions of the study area (Figure 1-1, Inset B).

We created a subset of the elevation grid using GIS by clipping the grid to an area defined by a 1 mile buffer from the park boundary. This defined a digital terrain model whose boundary corresponded to digital data layers supplied by DEWA personnel. All other terrain variables were derived from this digital terrain model. Since the digital terrain model records elevations directly, no additional processing was needed to define the elevation layer (Figure 1-1). We derived the remaining terrain variables from the elevation layer using various algorithms available in the Arc/Info software package (ESRI, Inc. Redlands, CA).

Aspect was generated from the digital elevation model by measuring the direction of the maximum rate of change (slope) calculated for a 3x3 window surrounding each cell (ESRI, Inc. 1994). The output of the aspect function is a compass bearing from 0-359 degrees for each cell. In order to make this measure useful in multivariate analysis, aspect was translated to a measure of northness by a cosine transformation so that aspect varies continuously from -1 (south) to 1 (north) (S. Weiss, Stanford Univ., pers. comm.) (Figure 1-2a.).

Slope (percent) was generated from the elevation matrix for each cell and measures the maximum rate of change in elevation from each cell to its neighbors (ESRI, Inc. 1994) (Figure 1-2b.). Conceptually, a plane is fitted over a 3x3 window of cells surrounding the cell of interest and the slope of the plane is calculated (Burrough 1986).

A measure of relative incident light striking the surface was calculated from the digital elevation model using the hillshade function in Arc/Info. This function allows for calculation of surface areas in direct sunlight, shade, and shadow given the elevation and azimuth of a light source (e.g., the sun). We calculated the sun's position and height above the horizon at the summer and winter solstice for our study area using tables provided by Marsh (1983). A mean relative solar radiance value was calculated by taking the by-pixel mean of these two surfaces. This calculated grid provided a measure of mean solar illumination during the year at each pixel relative to other pixels on the surface (values range from 0-255, are relative to the map, and do not reflect actual light reaching the surface) (Figure 1-2c.).

A measure of terrain shape was calculated from the digital elevation model following methods outlined in McNab (1989). The terrain shape index quantifies local convexity or concavity of a terrain surface. This measure is calculated using GIS as the difference between elevation at the center of a "moving window" and surrounding cells in the window. A moving window is generated by measuring attributes of a cell in relation to its neighbors in a matrix of cells; the next cell to the right is then processed in relation to its neighbors, and so forth. By varying the size of the window used to calculate the index, different scales of convexity and concavity can be measured. We used a circular moving window of 150m radius (5 cells on the DEM) to calculate terrain shape. We chose this window size after experimentation because it captured the prominent features at the scale of interest for our study area such as ravines and bench environments. Negative terrain shape values indicate a locally concave surface (e.g. a ravine) while positive values indicate a locally convex surface (e.g. a ridge or hummock). Values near zero indicate a locally flat surface (Figure 1-2d.).

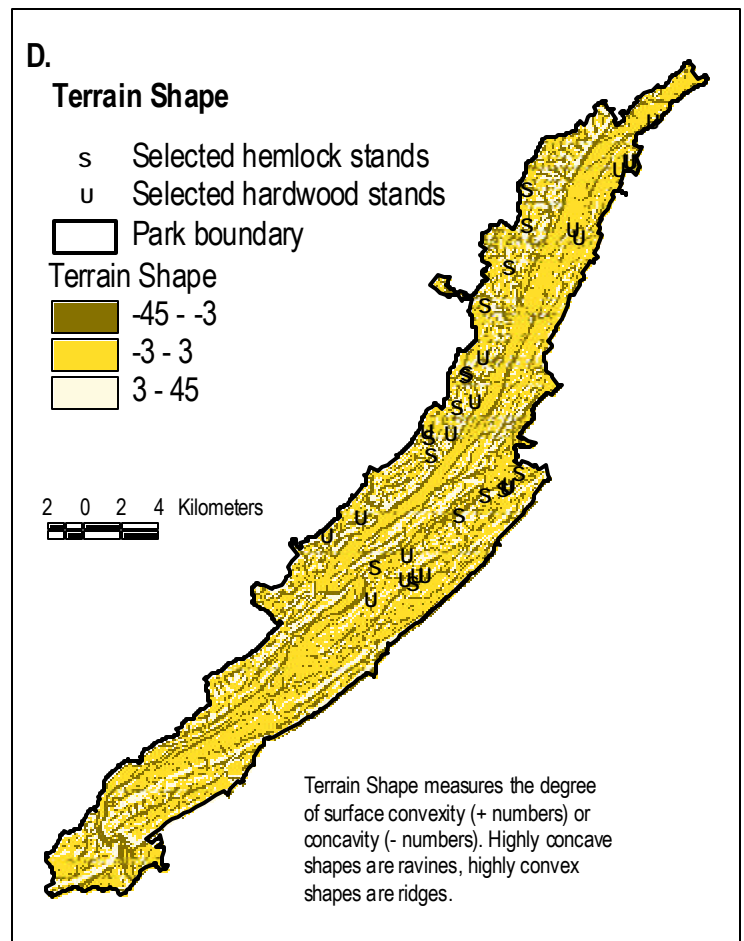
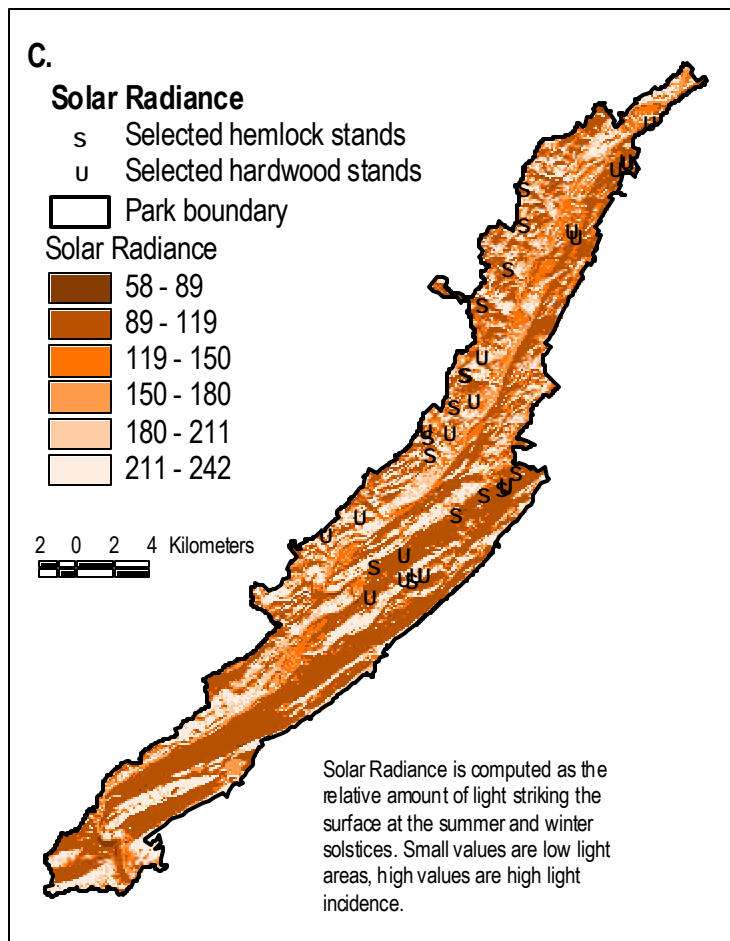
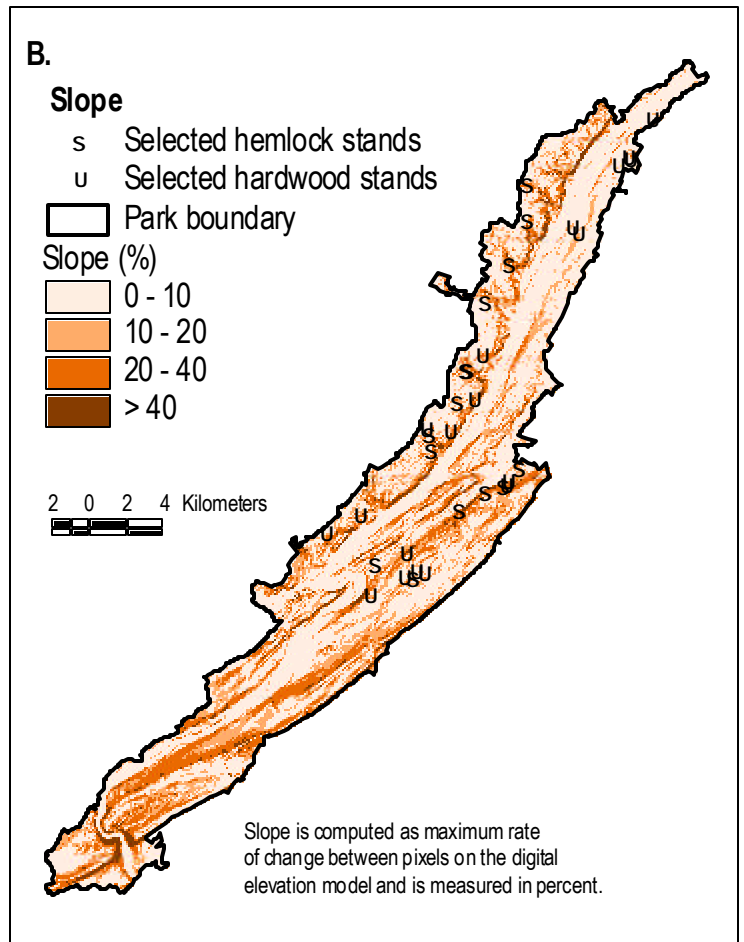
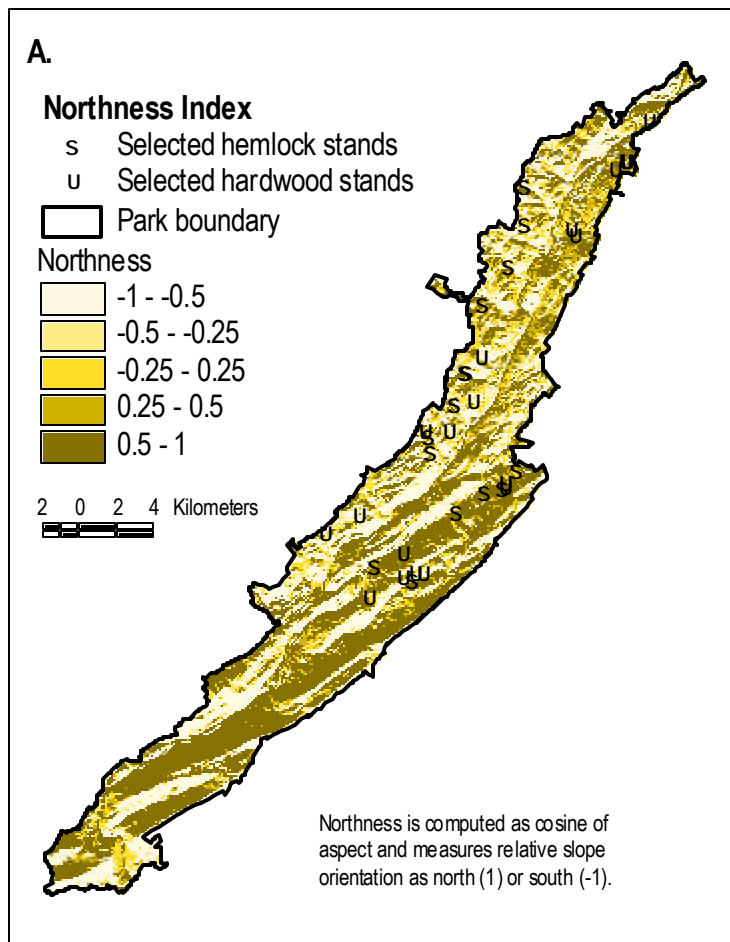


Figure 1-2. Terrain variables for Delaware Water Gap National Recreation Area used in sample design. Also shown are selected hemlock and non-hemlock study site locations.

We computed summaries of the elevation, slope, northness, terrain shape, and solar radiance terrain variables for all forest stands. This was accomplished using map overlay techniques to summarize the by-pixel terrain variables within each of the forest stand boundaries. Statistical summaries of the mean, variance, and range of pixel values were computed for each stand. We standardized the terrain variables to mean zero and unit variance by calculating z-scores for each of the terrain variable maps to eliminate bias due to different measurement units (Freund 1981).

Roads and streams were mapped by the US Geological Survey, National Mapping Division at 1:24,000 map scale. We augmented the stream map by calculating stream order for major tributary stream systems flowing into DEWA using the Strahler method (Strahler 1964).

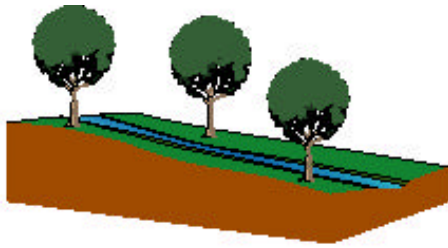
Statistical clustering and stratification

We used terrain variables described above to examine the range of environmental conditions where hemlock trees are found, and to determine terrain types that could be used to stratify field sampling. We used Euclidean distance-based K-means clustering in Systat (Wilkinson et. al 1998) to determine terrain types among 142 hemlock stands using 5 terrain variables.

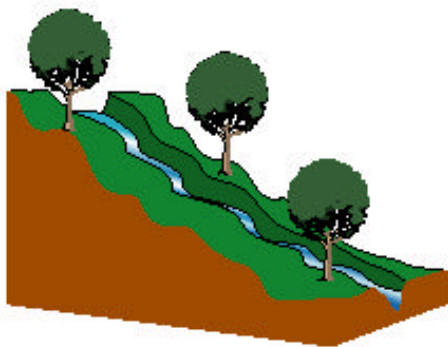
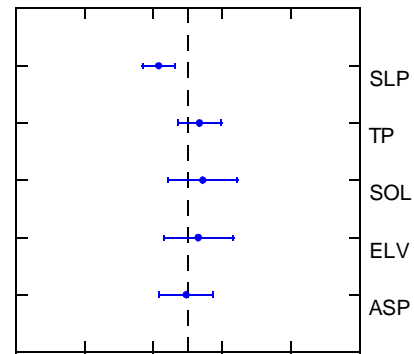
We initially clustered hemlock stands into 3-10 strata. Upon examination of profile plots and cluster means of terrain variables, we reduced the number of strata to 3. This provided easily interpretable groups of hemlock environments that captured the main terrain types where hemlock occurs in DEWA: ravine, bench, and mid-slope (Figure 1-3). The Aravine@type represents large, generally northwest trending, topographically concave drainages. The Abench@type represents gently sloping, topographically flat to slightly convex areas at moderately high elevations. The Amid-slope@type represents low incident light, steeply sloped, topographically convex areas that generally occur in the mid-slope regions of hillsides in the park.

To test for differences in biota based on vegetation, we needed to control for differences in two factors thought to be important for structuring aquatic communities: stream order and terrain. Thus, the overall design called for construction of a 2x2x3 block matrix based on two vegetation strata (hemlock forest/non-hemlock forest), 2 stream order strata (1st order/ 2nd order), and 3 terrain strata (bench/ravine/mid-slope) (Table 1-1). We used the stand-based vegetation map to construct 2 vegetation strata by classifying forest type as either hemlock or non-hemlock. We created 2 stream order strata by computing stream order for all streams within DEWA (described above) and intersecting the stream and vegetation maps in GIS using a map overlay technique. We then selected only those hemlock (N=56) and non-hemlock (N=333) forest stands from the vegetation map that were drained by 1st or 2nd order streams. The bench, ravine, and mid-slope terrain strata were constructed using clustering on 5 terrain variables as previously described.

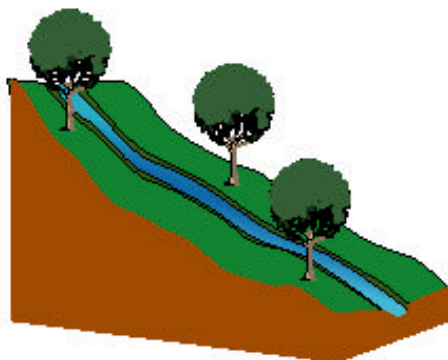
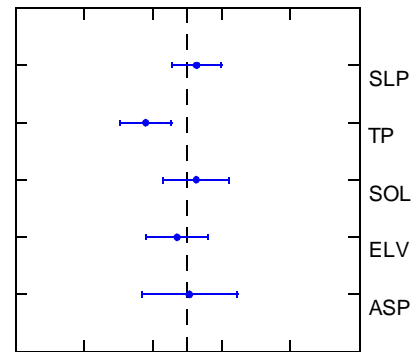
We defined 5 overall strata by combining terrain type and stream order. We were unable to completely fill the 2x2x3 sampling matrix as one of the terrain strata (Amid-slope@) did not contain streams of greater than 1st order. Combined terrain type/stream order strata (hereafter termed simply “stream types”) were assigned designations as follows: bench, stream order 1;



Bench sites - Low gradient, topographically flat to slightly convex areas with moderately high elevation



Ravine sites - Moderate to high gradient, topographically concave areas at lower elevations.



Mid-slope sites - Very steep, topographically convex areas with low light.

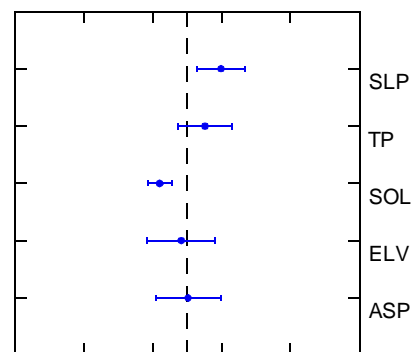


Fig. 1-3. Conceptual diagram of the 3 terrain strata sampled in DEWA (left) as defined by cluster analysis. Cluster profile plots (right) show the distribution of five topographical variables used in cluster analysis (SLP=slope, TP=terrain shape, SOL=solar radiance, ELV=elevation, and ASP=aspect). Dotted lines in cluster profile plot indicate the grand mean for each variable, circles indicate the within-cluster mean, and horizontal line indicates one standard deviation above and below the mean. Stream order was also considered as a criterion in selecting and pairing stream sites.

bench, stream order 2; ravine, stream order 1; ravine, stream order 2; mid-slope, stream order 1).

Table 1-1. Terrain and stream order strata defined for the landscape-based sample design, and number of replicate sample sites placed in each strata. Hemlock and hardwood sites in similar strata were paired for analysis to minimize influences from terrain and stream size. No mid-slope, stream order 2 sites were present on the landscape. One bench, second order pair was dropped during sampling *.

<i>Terrain strata</i>	Hemlock		Hardwood	
	<i>Stream order 1</i>	<i>Stream order 2</i>	<i>Stream order 1</i>	<i>Stream order 2</i>
Bench	3	3 *	3	3 *
Ravine	3	3	3	3
Mid-Slope	3	N/A	3	N/A

Within each of the resulting strata, we used a multivariate pairing method to find similar pairs of hemlock and non-hemlock stands. Our goal was to find pairs of stands where stream order was equivalent and differences between terrain variables were minimized, thus allowing us to observe differences in stream biota with “all else being equal”, to the extent possible. Stand pairing was accomplished by computing a multivariate Euclidean distance in S-Plus (Venables and Ripley 1994) between all possible pairs of hemlock forest stands and non-hemlock forest stands using mean terrain variables (elevation, slope, northness, terrain shape, and relative solar radiance) measured for each stand and summarized as z-scores. We sorted distances in ascending order and selected the 10 closest non-hemlock matches for each input hemlock stand. We then assessed each selected hemlock stand against the 10 potential hardwood matches for viability as matched pairs.

After generating lists of matched pairs of hemlock and non-hemlock forest stands within each combination of stream order and hemlock cluster, we met with park personnel to evaluate the feasibility of sampling each stand pair based on logistics and sampling considerations. These included access, stand size (only stands greater than 5 ha were selected), influence of human disturbance, beaver activity, other forest types upstream of the stand, and length of stream within the stand available for aquatic sampling. Using the generated list of paired stands, we were able to quickly find appropriate matched pairs that could be accessed by field crews and were similar in terrain and stream order, but different in vegetation type. Field inspection confirmed the strength of site similarity based on terrain, and led to selection of 15 pairs for sampling. One pair was discarded (bench, stream order 2) during Spring 1997 sampling due to clear differences in water flow. Timber cruises were also conducted in selected stands by personnel from Pennsylvania State University to assess vegetation composition and to check the accuracy of vegetation maps (Sullivan et. al. 1998).

RESULTS

Statistical summaries of elevation, slope, “northness”, terrain shape, and solar radiance computed for all forest stands (Table 1-2) show that hemlock stands generally occur in a lower elevation, higher slope, lower light environments (“northness” and relative solar radiance), and in more concave terrain shapes than hardwood forests. This finding is in line with expectations that hemlock occurs in more shaded environments, and persists in areas that were less accessible to past harvest activities. In general, selected forested stands had less within forest type terrain variance than among the overall population of hemlock and hardwood stands.

Table 1-2. Distribution of terrain variables among vegetation types within Delaware Water Gap National Recreation Area.

Forest type	Terrain variable	Minimum	Maximum	Range	Mean	Std. dev.
All hemlock	Elevation (m)	88.00	422.00	334.00	203.08	55.37
All non-hemlock	Elevation (m)	85.00	490.00	405.00	203.07	125.02
Selected hemlock	Elevation (m)	120.00	375.00	255.00	220.03	45.83
Selected non-hemlock	Elevation (m)	108.00	379.00	271.00	248.70	65.79
All hemlock	Slope (%)	0.00	99.39	99.39	25.82	16.99
All non-hemlock	Slope (%)	0.00	147.58	147.58	15.70	14.96
Selected hemlock	Slope (%)	0.59	87.90	87.31	26.13	15.69
Selected non-hemlock	Slope (%)	0.00	77.25	77.25	18.51	11.78
All hemlock	Northness index	-1.00	1.00	2.00	0.33	0.64
All non-hemlock	Northness index	-1.00	1.00	2.00	0.08	0.66
Selected hemlock	Northness index	-1.00	1.00	2.00	0.26	0.62
Selected non-hemlock	Northness index	-1.00	1.00	2.00	0.21	0.68
All hemlock	Relative solar radiance	58.00	241.50	183.50	129.89	44.64
All non-hemlock	Relative solar radiance	60.50	241.50	181.00	128.23	69.65
Selected hemlock	Relative solar radiance	73.00	241.00	168.00	132.85	41.77
Selected non-hemlock	Relative solar radiance	79.00	241.50	162.50	141.77	46.11
All hemlock	Terrain shape	-42.93	28.43	71.36	-2.24	8.36
All non-hemlock	Terrain shape	-39.09	44.41	83.49	0.42	5.18
Selected hemlock	Terrain shape	-34.30	21.72	56.01	-3.12	8.71
Selected non-hemlock	Terrain shape	-28.99	16.93	45.91	-0.56	5.28

Discriminant analysis conducted on hemlock stands clustered into terrain strata confirmed the strength of group membership (Table 1-3). Discriminant analysis tests the separation of observations into previously defined groups and can be used as a check on multivariate classification (Davis, 1986). Overall classification accuracy was 99 percent, with only two

stands out of 142 mis-classified. This result confirms that terrain strata were strongly defined. An evaluation of the matched hemlock and hardwood stands revealed that, on average, hemlock stands were more similar in terrain to matched hardwood stands than to other hemlock stands grouped in the same terrain strata. Multivariate distances generated between hemlock stands and matched hardwood stands were generally smaller (i.e. more similar) when compared to multivariate distances computed among hemlock stands within the same terrain strata (see example in Figure 1-4).

Table 1-3. Results of discriminant function test on hemlock stand clusters showing strength of group membership. Table shows observations classified from cluster analysis (rows), predicted group membership based on discriminant function test (columns), and between group F statistic in parentheses. Only two observations were predicted to be in classes other than those assigned from clustering. Overall classification accuracy was 99 percent.

<i>Terrain Strata</i>	Predicted Group Membership			<i>%correct</i>
	<i>1 (bench)</i>	<i>2 (ravine)</i>	<i>3 (mid-slope)</i>	
1 (bench)	62 (0.0)	0 (32.309)	1 (50.955)	98
2 (ravine)	0 (32.309)	35 (0.0)	1 (37.998)	97
3 (mid-slope)	0 (50.955)	0 (37.998)	43 (0.0)	100
Total	62	35	45	99

Sites selected and sampled for aquatic macroinvertebrates and fish are shown in Figure 1-6. Additionally, automated temperature loggers were placed in a subset of sites and retrieved after 1 year of hourly data collection (discussed fully in Chapter 4). Locations of temperature loggers are shown graphically in Figure 1-6. Coordinates, site numbers, stream name, and site pairs for all sites sampled for macroinvertebrates and fish are listed in Appendix 1-A.

DISCUSSION

The landscape-based stratified-pair design was successful in representing the range of terrain variation in DEWA and in minimizing the confounding influence of landscape variation between paired sites. Terrain variable means were not markedly different between 14 selected hemlock stands and the 127 non-selected hemlock stands (Figure 1-5), or between 14 selected non-hemlock stands and the 2,131 non-hemlock forest stands left unselected (Figure 1-5). Overall terrain variable distributions show greater ranges than the stands selected for sampling, due primarily to stands found on ridge tops or near river bottoms that would have been logistically difficult to sample.

Because this sampling design is meant to highlight differences in aquatic systems due to vegetation differences, the accuracy of vegetation information used to select stands is important. Data collected by Pennsylvania State University (Sullivan et. al. 1998) in stands we selected

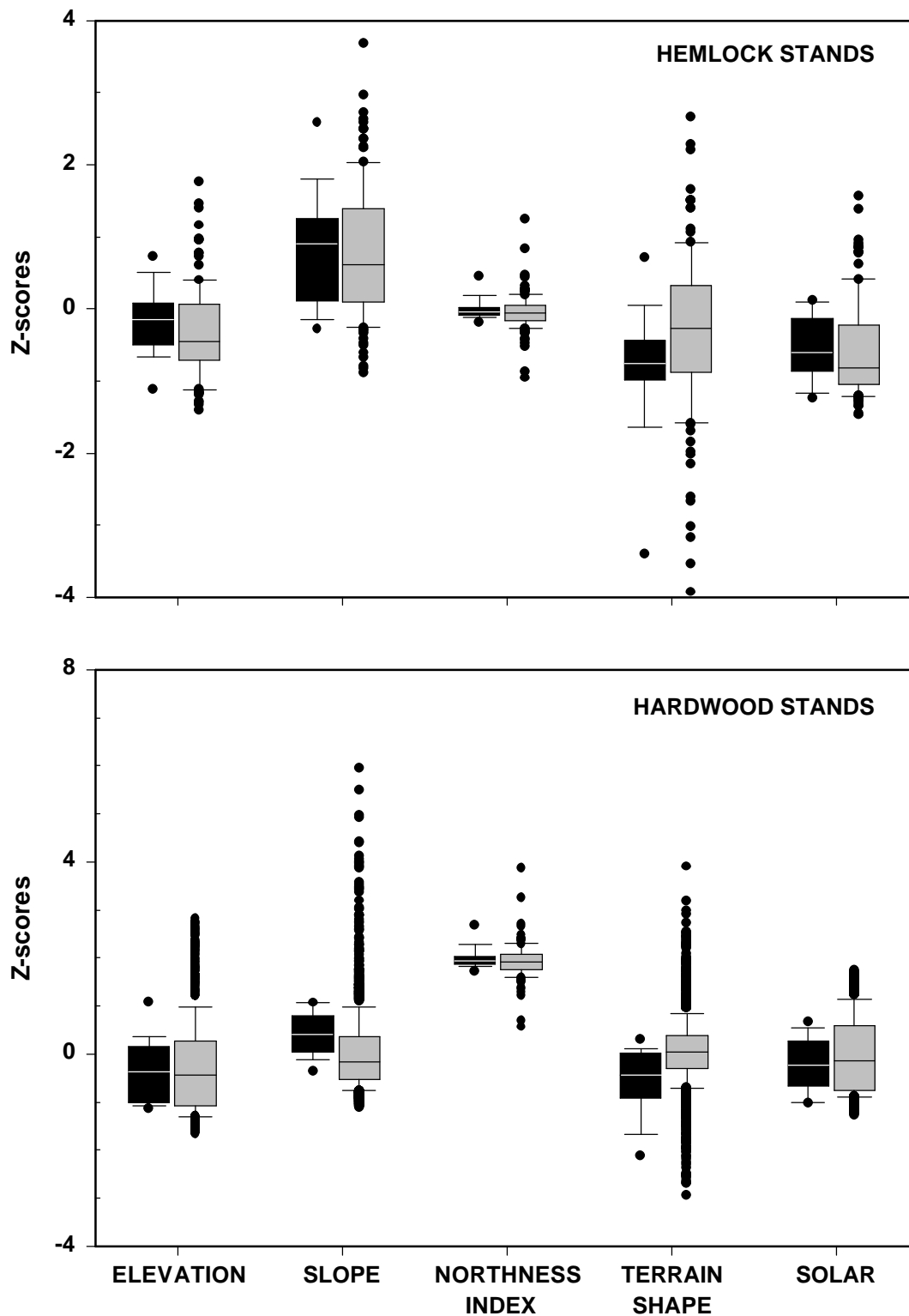
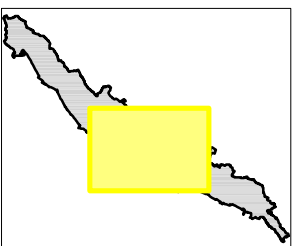


Figure 1-5. Comparisons of the distributions of the five terrain variables between selected (black boxes) and non-selected (gray boxes) stands. Top panel compares hemlock stands and bottom panel compares hardwood stands. Boundaries of the box mark the 25th and 75th percentile, the line within the box marks the median, and the whiskers mark the 10th and 90th percentiles. Symbols represent values lying outside the 10th and 90th percentiles.

North Section



LEGEND:

1.13

demonstrates that vegetation composition was consistent with the *a priori* classification from vegetation maps produced by Myers and Irish (1981). Since we defined a hemlock stand as containing hemlock in either the primary, secondary, or tertiary forest component, we expected to have mixed composition stands in our analysis. Results from Sullivan et. al. (1998) indicate that stands classified as hemlock contained at least 24% basal area in hemlock and as much as 75% hemlock; typically, hemlock classified stands had 53% basal area in hemlock. Furthermore, the amount of hemlock in hemlock stands was consistently greater than its hardwood stand pair. The amount of hemlock basal area in a stand classified as hemlock was between 2 and 27 (and typically 13) times that of its hardwood stand pair (Sullivan et. al 1998).

Although this sampling scheme is based on classical sampling designs (e.g. randomized blocks), it incorporates aspects of more recent designs as well. This design allows for inclusion of landscape variation measured through use of GIS (sensu “gradsect” sampling: Gillison and Brewer 1985), as well as pairing to control for possible confounding variables (sensu case-control sampling; Schlesselman 1982). First, we used easily obtainable *a priori* information on terrain and vegetation to characterize hundreds of hemlock and non-hemlock forest stands within the park. Then we used this characterization to define landscape-based strata and to match pairs of hemlock and hardwood stands before field sampling. Evaluation demonstrates that this methodology was successful in capturing the range of terrain conditions in the park (Figure 1-5), in defining ecologically meaningful sampling strata (Table 1-3), and in finding closely matched hemlock-hardwood pairs (Figure 1-4). Subsequent chapters evaluate whether the design was ultimately successful in controlling confounding variation in observed aquatic community differences.

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Appendix 1-A.

Sample site locations:

Site #¹	Stand²	Stream Name	Easting³	Northing³	Site Pair
042201	142	Shimers	518085.44	4573432.30	102211
051101	243	White Brook	517085.73	4571380.38	271111
072113	365	Conoshaugh	511424.98	4569959.43	222103
081102	529	Unnamed	513961.29	4567521.61	271112
083102	561	Unnamed	514157.01	4567332.15	273112
092112	485	Dry Brook	511492.68	4567552.97	152102
102211	657	Adams	510851.62	4565439.65	42201
111113	822	Dingmans	509375.98	4563553.52	271103
152102	1020	Unnamed	509338.23	4560689.94	92112
152213	1059	Hornbecks	507621.81	4559863.56	232203
162101	1202	Unnamed	508611.86	4558474.17	192111
172212	1191	Spackmans	507912.15	4557922.76	182202
182202	1327	Unnamed	507428.47	4556803.31	172212
191202	1335	Tumbling Waters	506283.37	4556880.46	291212
191211	1368	Tumbling Waters	506254.13	4556689.57	291201
192111	1449	Broadhead Cr.	506650.45	4555529.59	162101
222103	1784	Unnamed	502660.60	4551986.72	72113
232203	1850	Unnamed	500790.60	4551029.33	152213
271103	1909	Flat Brook tributary	504278.32	4549125.51	111113
271111	1509	Flat Brook tributary	510608.64	4554870.85	51101
271112	2037	Flat Brook tributary	503467.41	4549556.08	81102
273103	1614	Flat Brook tributary	510430.96	4554196.60	273113
273111	1673	Flat Brook tributary	509327.98	4553646.15	283101
273112	1653	Buttermilk Falls	510225.20	4553959.57	83102
273113	1742	Flat Brook tributary	507761.49	4552642.15	273103
283101	2204	Unnamed	503096.20	4547903.67	273111
291201	2035	Vancampens Brook	505862.37	4549032.81	191211
291212	2107	Vancampens Brook	505583.78	4548828.72	191202

¹ Site numbers were generated by USGS-BRD, are hierarchically structured, and represent stream drainage # (digits 1-2), terrain type (digit 3, 1=bench, 2=ravine, 3=mid-slope), stream order (digit 4), vegetation type (digit 5, hemlock =0, hardwood = 1), and replicate number (digit 6).

² Stand numbers were generated by USGS-BRD from polygon codes contained in vegetation map provided by Delaware Water Gap NRA personnel (Myers and Irish, 1981).

³ Coordinates are expressed in Universal Transverse Mercator (UTM) format, Zone 18, using NAD27 geodetic datum.

Chapter 2: Influence of eastern hemlock (*Tsuga canadensis*) on stream invertebrate community structure in small headwater streams of the Delaware Water Gap National Recreation Area.

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INTRODUCTION

It has become increasingly clear that the physical and biological structure of streams are inextricably linked to the status and condition of the surrounding watershed. For example, terrestrial leaf litter constitutes the main energy supply for forested headwater streams (Hynes 1975), and riparian vegetation acts synergistically with topography to influence instream habitat conditions (Bisson et al. 1987) and organic carbon and nutrient processing rates (Pinay et al. 1990). In turn, aquatic macroinvertebrates are primary consumers of terrestrial leaf litter and their distribution and production have been shown to correlate with components of the surrounding forests (Ross 1963). In addition, aquatic invertebrates represent a significant food source for fish and their feeding activity modifies the form and rate with which leaf material is processed and exported (Cuffney et al. 1990). Therefore, changes in macroinvertebrate community structure associated with forest disturbances may cascade to other aquatic assemblages. Furthermore, since emerging insects represent a significant energy source for birds, spiders and other terrestrial fauna (Jackson and Fisher 1986), macroinvertebrate responses may feed back to the terrestrial system as well. Thus, forest disturbance may have profound effects to the aquatic macroinvertebrate community and to the overall watershed ecosystem. However, most research has emphasized the short-term effects of forest removal on stream communities. There have been relatively few studies specifically designed to examine the long-term consequences of changing forest composition on stream communities (but see Molles 1982, Stout et al. 1992).

In this chapter, we compared aquatic macroinvertebrate community structure and composition in streams draining hemlock and mixed hardwood forests in an effort to predict long-term consequences of hemlock decline due to hemlock woolly adelgid (HWA). Orwig and Foster (1998) found stands suffering severe HWA-induced mortality in Connecticut showed little hemlock regeneration because small trees were disproportionately affected by HWA, and predicted a succession to mixed hardwood in affected stands. In addition, many of the hardwood-dominated catchments in Delaware Water Gap National Recreation Area (DEWA), particularly in ravine environments, were once hemlock but were replaced by mixed hardwoods following logging over 100 years ago (Sullivan et al. 1998). Therefore, we believe long-term predictions based on this comparative study reflect realistic assumptions regarding long-term changes in forest composition due to HWA. The specific mechanisms by which hemlock influences biological structure of both fish and aquatic invertebrates are explored in Chapter 4.

METHODS

Collection of Invertebrate Samples

We used the landscape-based, stratified pair sampling design described in Chapter 1 to select sites for collecting aquatic invertebrate samples. Invertebrate sampling was conducted during the first two weeks of April 1997 prior to spring emergence when benthic diversity is typically highest in small streams (Resh and McElravy 1993). Samples from streams of each hemlock/hardwood site pair were collected either on the same day or only one day apart to control for temporal differences in community structure. Sample reaches were defined by a distance of 80 meters for 1st order streams and 160 meters for 2nd order streams. These distances were selected because, on average, they represented approximately 40 mean stream widths and encompassed a minimum of three riffle-pool sequences in DEWA. Such areas have been found to be sufficient for measuring fish diversity (Lyons 1992, Angermeier and Smoger 1995) and consequently should be more than adequate for benthic invertebrates.

Two approaches were used for invertebrate sampling. Firstly, random sampling was used to obtain unbiased estimates of actual and relative abundances. A total of 20 equally spaced transects perpendicular to stream flow were established (i.e., 4 meters apart for the 80 meter 1st order reaches, and 8 meters apart for the 160 meter 2nd order reaches). At each transect, stream width was measured to the nearest 0.3 meters (i.e., opening of the standard D-frame kick net used in sampling) for all transects. Subsequently, a random number was generated between 0 and the stream width in 0.3 meter units using either a random number table or calculator. This number was rounded up and used to determine the location of a single sample site along each of the 20 transects. Sampling consisted of 30-second kicks with a standard D-frame kick net (net mesh = 250 microns) over an area of 0.09 m² at each selected site. All 20 samples were initially composited in 5-gallon buckets, and upon completion, placed into as many 1-liter nalgene sample jars as needed. Samples were preserved with 80% isopropyl alcohol in the field. Composite samples allowed us to maximize sampling effort among, as well as within, streams at the expense of assessing within-stream variability. Since we were interested in comparing biological structure among stream types, as opposed to reaches within a single stream, we believe composite sampling was justified.

Secondly, a qualitative, microhabitat-based approach was used to maximize the probability of collecting individuals of all species by ensuring sampling was conducted in all available microhabitats independent of their rarity. Available microhabitats were defined by combinations of water depth, velocity, substrate, and turbulence (Table 2-1). Two investigators (1 on each bank) searched the entire stream reach for the presence of each of the 50 possible microhabitat types. Attempts were made to collect a minimum of two samples from each available microhabitat type. Qualitative samples were also collected with a D-frame kick net. Every effort was also made to sample each microhabitat type well. This did not mean equal time because some microhabitat types were much easier to sample than others. For example, microhabitat types with leaf pack substrates required little time because leaf packs could be quickly removed and placed into the collecting net. Identity and number of all microhabitat types were also recorded. Resulting samples were composited as described above for random samples.

Table 2-1. Microhabitat matrix used to stratify qualitative sampling. Checked boxes refer to microhabitat types observed in DEWA streams.

Substrate	Slow-water habitats		Fast-water habitats		
	Depth <30 cm	Depth >30 cm	Fast/ turbulent	Fast/non- turbulent	Water falls
Logs (>30 cm)					
Sticks (<30 cm)					
Leaf packs					
Needle packs					
Moss					
Silt/detritus (Not mineral)					
Sand (mineral: <pea sized)					
Gravel (mineral:pea-golf ball-sized)					
Cobble (mineral golf ball-head-sized)					
Boulder/bedrock (mineral:>head-sized)					

Laboratory Processing of Invertebrate Samples

Processing samples consisted of three phases: 1) a washing/floating phase designed to eliminate larger debris from the sample and separate the sample into organic and mineral fractions for easier picking (i.e., removing organisms from debris); 2) a subsampling phase designed to partition the composite samples into smaller units; and 3) the actual picking and preservation of invertebrates from remaining debris. Each of these phases is described in detail below:

Washing/floating phase. Initially, samples were poured into a large pan and the larger leaves and stones washed over a 250 micron sieve. Washed stones and leaves were returned to sample containers and preserved. A percentage of the resulting stone-leaf fractions were examined for missed insects to determine the efficiency of the washing phase (i.e., number of invertebrates found in stone-leaf fraction following washing relative to the total number of invertebrates found in the entire sample; mean observed efficiency was 85%). Invertebrates and smaller material

retained by the sieve were floated with a stream of water to separate invertebrates and organic debris from mineral material. Completion of this task resulted in an organic fraction that contained finer particulate organic matter and most of the invertebrates, and a mineral fraction containing largely sand, gravel, and some of the heavier invertebrates such as case-making caddisflies. Both organic and mineral fractions were subsequently subsampled as described below prior to picking.

Subsampling Phase. Composite samples contained huge numbers of individuals and so only a portion of each sample could be picked for identification. Consequently, some method of partitioning each sample into equal portions, and randomly selecting subsamples for picking was required. To do this, we fabricated a device that splits a sample into two equal fractions (by volume). The sample splitter consists of hinged bucket, a wedge, and two receiving receptacles. For each sample, the mineral and organic fractions were split separately as follows: Fractions were placed into the pouring bucket, the buckets tipped over the wedge, and the two subsamples collected. Each fraction was split into 16 subsamples and four of them (i.e., 25% of the total) were selected at random to pick. The 25% was chosen based on the results of a power analysis conducted on preliminary samples (i.e., the organic and mineral fraction from two samples). The power analysis was conducted for the total number of taxa and total number of individuals using a bootstrapping method of randomization (Manly 1991). We wrote a computer algorithm in S-Plus (Venables and Ripley 1994) that randomly drew a number of subsamples (one, two, four or eight) from the total ($N=16$), calculated the value of the response variable, and compared it to the true value from the entire sample. This process proceeded for at least 100 iterations and a distribution of differences was generated from the difference between the response from bootstrapped subsamples and that of the total sample. Using this approach, we found that data generated from four randomly selected subsamples (i.e., 1/4 of the total composite sample) was representative of the entire sample in terms of taxa richness and total abundance. That is, species richness and total abundance in the four subsamples was within 10% of that in the entire sample at least 95% of the time.

Picking and Preservation. Selected subsamples were picked in white enamel pans under a 1.25X magnifying lamp. Invertebrates and the remaining debris were preserved separately in 50% isopropyl alcohol. A fourth of the debris samples ($n=14$) were re-examined to determine efficiency during the picking phase (mean=91%). Where possible, all invertebrates were identified to the species level using appropriate keys. Count data from both mineral and organic fractions were then pooled for each sample and tabulated. A voucher collection was also created.

Data Summarization

A total of 184 taxa were positively identified from benthic samples; 85 taxa were identified to species, 90 to genus, 8 to family and 1 to order (Appendix 2-A, in this document and on attached diskette). However, as is typical with benthic samples, there were many uncertainties that forced us to edit the invertebrate data set prior to analysis. For example, although there were many taxa that were positively identified to species, in many instances there were samples that contained individuals of the same genus, but for various reason (e.g., specimens too small or key

morphological features missing) we were unable to identify them to species. Thus, to prevent overestimating diversity we were forced to lump all such individuals, whether identified to species or genus, at the genus level. The alternative would have been to count those specimens identified to genus as a separate taxa from those identified to species. For example, individuals keyed to *Baetis* sp. may or may not have been *Baetis tricaudatis*. To count both as separate taxon could potentially overestimate diversity and confound our analyses. A similar convention was used at all taxonomic levels. Therefore, analyses designed to detect hemlock effects on diversity were conservative. That is, because we probably under-represented diversity in our analyses, there may have been a larger forest type effect on diversity than reported here. The resulting data set contained a total of 151 taxa that were used for all subsequent analyses.

Two primary data matrices were created from the invertebrate samples and used for analyses. For those analyses based on species abundances (e.g., density and relative abundance comparisons), we used the site by species abundance matrix generated from the random samples only (Appendix 2-B, attached diskette). For those analyses based on occurrence or richness of species, we created a presence-absence matrix using data from both the random and qualitative samples (Appendix 2-C, attached diskette).

Secondary matrices were derived from the two primary matrices described above to compare trophic and taxonomic composition. For taxonomic composition, the number of individuals (derived by collapsing the site by species abundance matrix) and number of species (derived by collapsing the site by species presence-absence matrix) were determined for each of the following six taxonomic groups: Ephemeroptera, Plecoptera, Trichoptera, midge larvae, other insect taxa, and non-insect taxa. Similarly, for trophic composition, number of individuals and number of species were determined for each of the ten trophic classes used by Merritt and Cummins (1996): shredder-chewer, shredder-detritivore, shredder-gouger, collector-filterer, collector-gatherer, scraper, macrophyte-piercer, predator-engulfer, predator-piercer, and parasite. This suite of groups was reduced to seven because 3 groups (i.e., shredder-gouger, macrophyte-piercer, and parasites) were either not represented, or represented by only a few individuals. However, many species have been found to use several feeding modes (Appendix 2-A). Thus, for a given taxon at a given site, the number of individuals and number of taxa were weighted by the number of trophic classes assigned to that species. For example, if a given taxon was assigned to both scraper and predator-engulfer trophic classes, then for each site the number of individuals in the abundance matrix or the number of species in the presence/absence matrix would be divided by 2. Subsequently, all values within a trophic class were summed to obtain the total number of individuals or species of a given trophic class.

Data Analysis

We compared four community structure and three community composition metrics between streams draining hemlock and those draining hardwood forests (Table 2-2). Making use of the stratified pair design (see Chapter 1), we tested the null hypothesis that the difference in each community structure metric between site pairs was equal to zero (i.e., $p > 0.1$). That is, for each metric, we calculated the difference between individual hemlock-hardwood site pairs by

subtracting the value measured in the hemlock site from that in the corresponding hardwood site. We used general linear modeling to 1) test whether mean differences between forest types varied among stream types, and 2) test whether mean differences between forest types was equal to zero. Differences tended to be normally distributed so no transformations were required prior to analysis.

Table 2-2. Biological response variables compared between streams draining hemlock and hardwood forests within DEWA.

<u>Community Structure</u>	
Taxa Richness	Total number of taxa
Shannon-Weiner Taxa Diversity Index	Metric that incorporates information on both taxa richness and the evenness with which taxa are distributed. Calculated as: $H' = -\sum p_i \log p_i$, where H' = Shannon Index, and p_i is the proportion of individuals occurring in taxon i .
Total Density	Total number of individuals per square meter.
Number of Rare Taxa	Rare taxa defined as those occurring at three sites or fewer.
<u>Community Composition</u>	
Trophic Composition	Proportion of taxa in each of the following seven trophic categories: shredder-chewers, shredder-detritivore, collector-filterer, collector-gatherers, scrapers, predator-engulfers, predator-piercers.
Taxonomic Composition	Proportion of taxa in each of the following six taxonomic categories: Ephemeroptera, Plecoptera, Trichoptera, Midge (i.e., Chironomidae), other insects, other non-insect taxa.
Taxa Occurrence	Proportion of sites in which each taxon occurs; calculated separately for each taxon.

We used multi-response permutation procedures (MRPP) to compare the proportion of taxa in each of the seven trophic and six taxonomic groups between streams draining hemlock and those draining hardwood forests. We also used MRPP to test for biological differences among the three terrain strata and two stream orders. For this analysis, we used proportions rather than count data to remove the effect of differences in taxa richness and focus on compositional differences. MRPP is a non-parametric procedure similar in purpose to discriminant analysis but has the advantage of not requiring multivariate normality and homogeneity of variance that are seldom met with ecological community data (McCune and Mefford 1995). Cases where the multivariate response was significant, we used the Kruskal-Wallis one-way ANOVA to test whether the proportion of individual trophic or taxonomic groups differed among forest or stream types.

We used logistic regression to conduct an odds ratio test that estimates the association between the occurrence of each taxon and forest type. The odds of taxon presence is the probability of presence divided by the probability of absence. There are two relevant odds: one specific to hemlock stands and the other specific to hardwood stands. The ratio of these odds is the odds ratio. The natural log of the odds ratio makes the statistic easily interpretable. In our case, log-odds ratio less than zero indicated taxa association with hardwood; whereas, ratios greater than zero indicate an association with hemlock. We computed odds ratios and p-values using LogXact (Mehta and Patel 1996).

Based on the results of the odds ratio test, we were interested in whether those taxa found to be associated with hemlock were a random subset of the community, or if they were taxonomically or functionally different. We used Fisher's Exact Test to test the hypothesis that trophic and taxonomic groups were equally represented among taxa associated with hemlock and those not associated with hemlock. We used StatExact (Mehta and Patel 1997) to calculate Fisher's test statistics and exact p-values.

RESULTS

Invertebrate Community Structure and Composition

We observed a significant forest type effect on all four community structure statistics examined. Overall, hemlock had a positive effect on total taxa richness and Shannon species diversity index, and a negative effect on total abundance and rare taxa richness (Fig. 2-1, pooled strata). Taxa richness was on average 37% higher in streams draining hemlock forests, and Shannon diversity index was about 9% higher on average. In contrast, streams draining hardwood forests supported an average of 42% more individuals (total density) than streams draining hemlock. Likewise, the number of rare species (i.e., those that occurred at fewer than 3 sites) were on average 67% more common in streams draining hardwood forest.

The significance and magnitude of the hemlock effect depended on stream type for species richness (ANOVA, $F=3.265$; $df=4,9$; $p=0.065$) and Shannon diversity index ($F=3.905$; $df=4,9$; $p=0.042$) but not for density and number of rare taxa ($p>0.25$ for both). However, for all four community structure metrics, 1st order, mid-slope sites responded differently than the other stream types, either showing no forest type effect, as with total richness, density, and rare taxa richness; or the opposite effect of the other stream types, as with Shannon diversity index (Fig. 2-1). Consequently, the pooled effect was examined with and without that stream type included. After removing 1st order mid-slope sites, the forest type effect (i.e., difference between site pairs) was no longer dependent on stream type for total taxa richness ($F=2.426$; $df=3,7$; $p=0.151$) or Shannon diversity index ($F=1.417$; $df=3,7$; $p=0.316$). Therefore, these results suggest a significant overall forest type effect on all four community structure metrics except in 1st order, mid-slope sites. Also, the fact 1st order mid-slope sites had significantly higher Shannon diversity in streams within hardwood forests but no difference in total richness between forest types suggests higher dominance in the hemlock sites for this stream type. That is, the distribution of individuals was less evenly distributed among species in the hemlock sites.

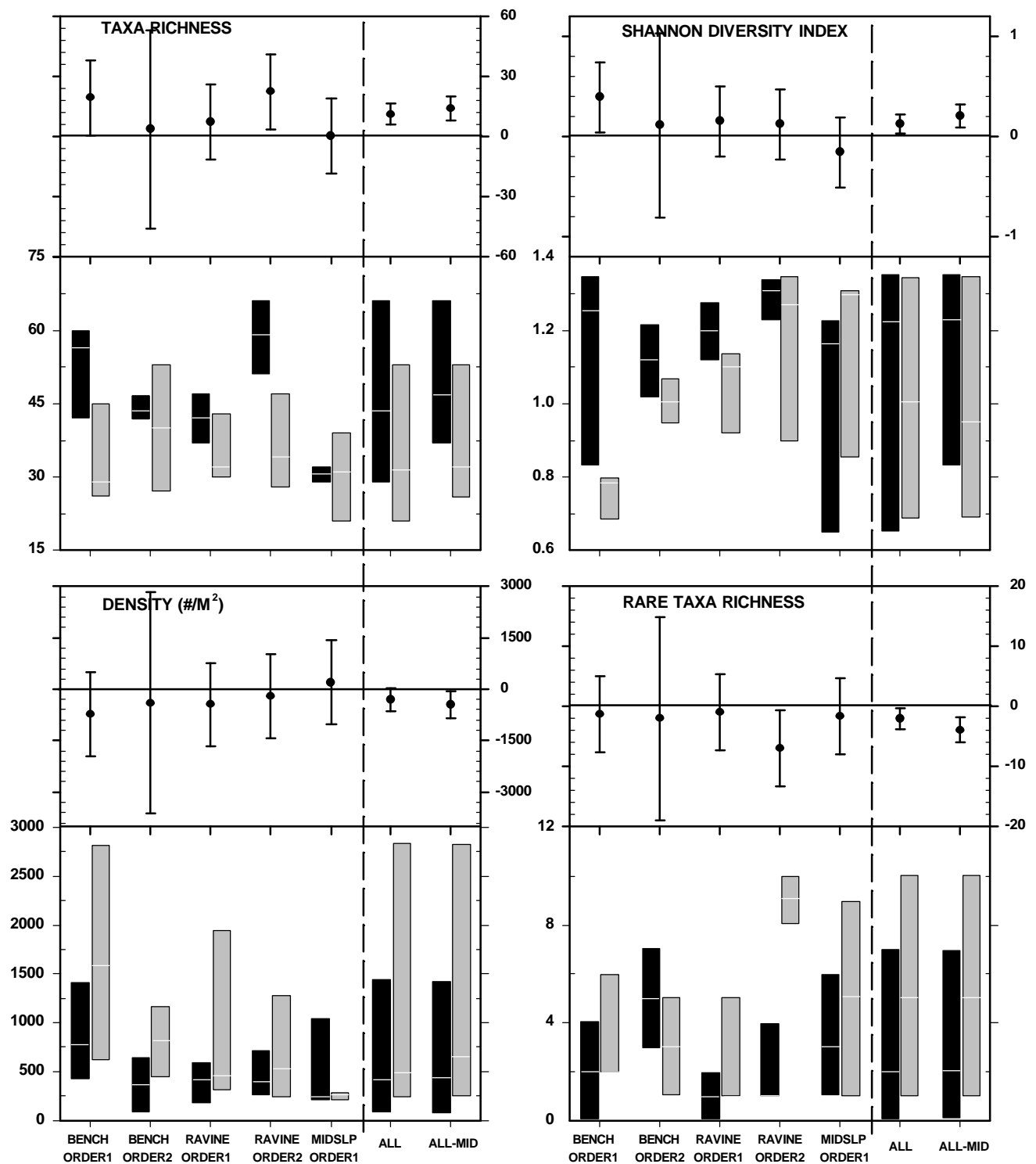


Figure 2-1. Comparison of four community structure metrics between streams draining hemlock and hardwood forests. Top panel shows mean differences (+/- 90% C.L.) between hemlock-hardwood site pairs. Positive values indicate higher means for hemlock. Bottom panel compares the range of values (limits of box) and medians (white line) between forest types (hemlock=black bars). Comparisons are made within each stream type as well as pooled across stream types (ALL) and all but midslope sites (ALL-MID).

More detailed comparisons of the composition of the invertebrate community revealed three important patterns. Firstly, trophic composition of the invertebrate community was significantly different between streams draining hemlock and hardwood forests as well as between the two stream orders (Table 2-3). Observed differences in trophic structure was not significant between terrain types. In streams draining hemlock, predator-engulfers represented a larger proportion and scrapers a smaller proportion of the invertebrate community in both 1st and 2nd order streams (Fig. 2-2). In contrast, taxonomic differences were only observed among terrain types (Table 2-3). Mayflies (Ephemeroptera) represented a larger proportion of the community in ravines, stoneflies (Plecoptera) in mid-slope sites, and midges in bench sites (Fig. 2-3). No hemlock effect on taxonomic composition was observed. These data indicate the higher taxonomic richness and diversity observed in streams draining hemlock were associated with distinct differences in trophic composition.

Table 2-3. Results of MRPP to test for proportional differences in trophic and taxonomic composition between forest type, terrain type, and stream order.

Stratum	<u>Trophic Composition (7 groups)</u>		<u>Taxonomic Composition (6 groups)</u>	
	MRPP statistic	P value	MRPP statistic	P value
Forest type (hemlock/hardwood)	-3.882	0.004	0.389	0.590
Terrain type (bench, ravine, mid-slope)	-1.322	0.102	-1.925	0.044
Stream order (1 st , 2 nd order)	-1.755	0.061	0.517	0.650

Secondly, a large number of taxa (n=15) occurred significantly more often in streams draining hemlock forests than those draining hardwood forests (i.e., strong hemlock associates, Fig. 2-4). Although 15 taxa may be within the range expected to show significant differences due to chance, the fact that all were associated with hemlock suggests forest type preferences. Of the 15 taxa, only three were found to occur only in streams draining hemlock (Table 2-4). However, the extent to which streams that drain hardwood forests contained strong hemlock associates seemed to be, in part, related to the proximity of the stream to hemlock. That is, the number of strong hemlock associates found in hardwood sites was inversely related to the distance to the nearest hemlock site, at least for a large fraction of the sites (Wald statistic:11.47, df=1, p=0.001; Fig. 2-5).

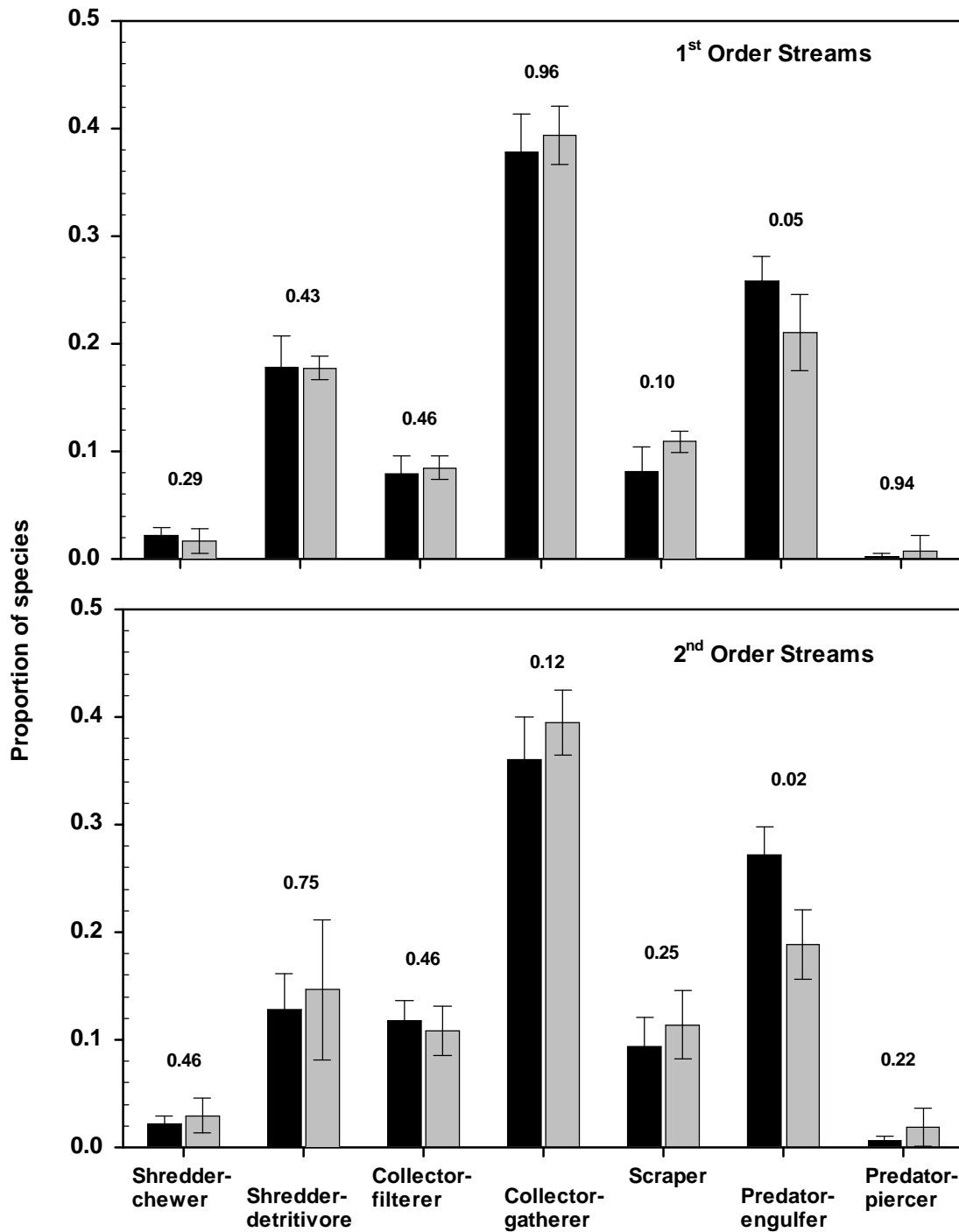


Figure 2-2. Comparison of stream invertebrate trophic structure between streams draining hemlock (black bars) and hardwood (gray bars) forests. Vegetation comparisons (mean proportion of species \pm 90% C. L.) are made within each stream order because stream order was also found to influence trophic composition (see text). No differences were observed among terrain types. Numbers above bars are p-values from Kruskal-Wallis one-way ANOVA with 2 d.f.

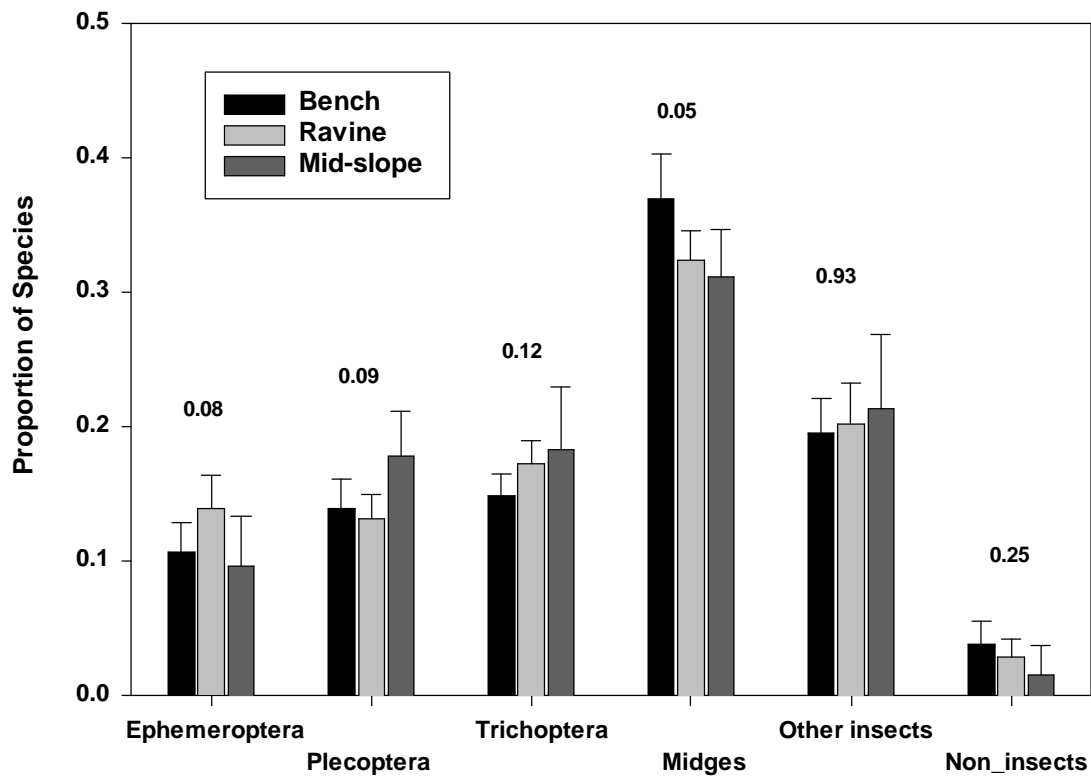


Figure 2-3. Comparison of stream invertebrate taxonomic composition between terrain types. No differences in taxonomic composition was observed between vegetation types or stream order (see text). Mean proportion of each taxa and associated 90% confidence limits are presented for each terrain type. Number above bars are p-values from Kruskal-Wallis one-way ANOVA with 2 df.

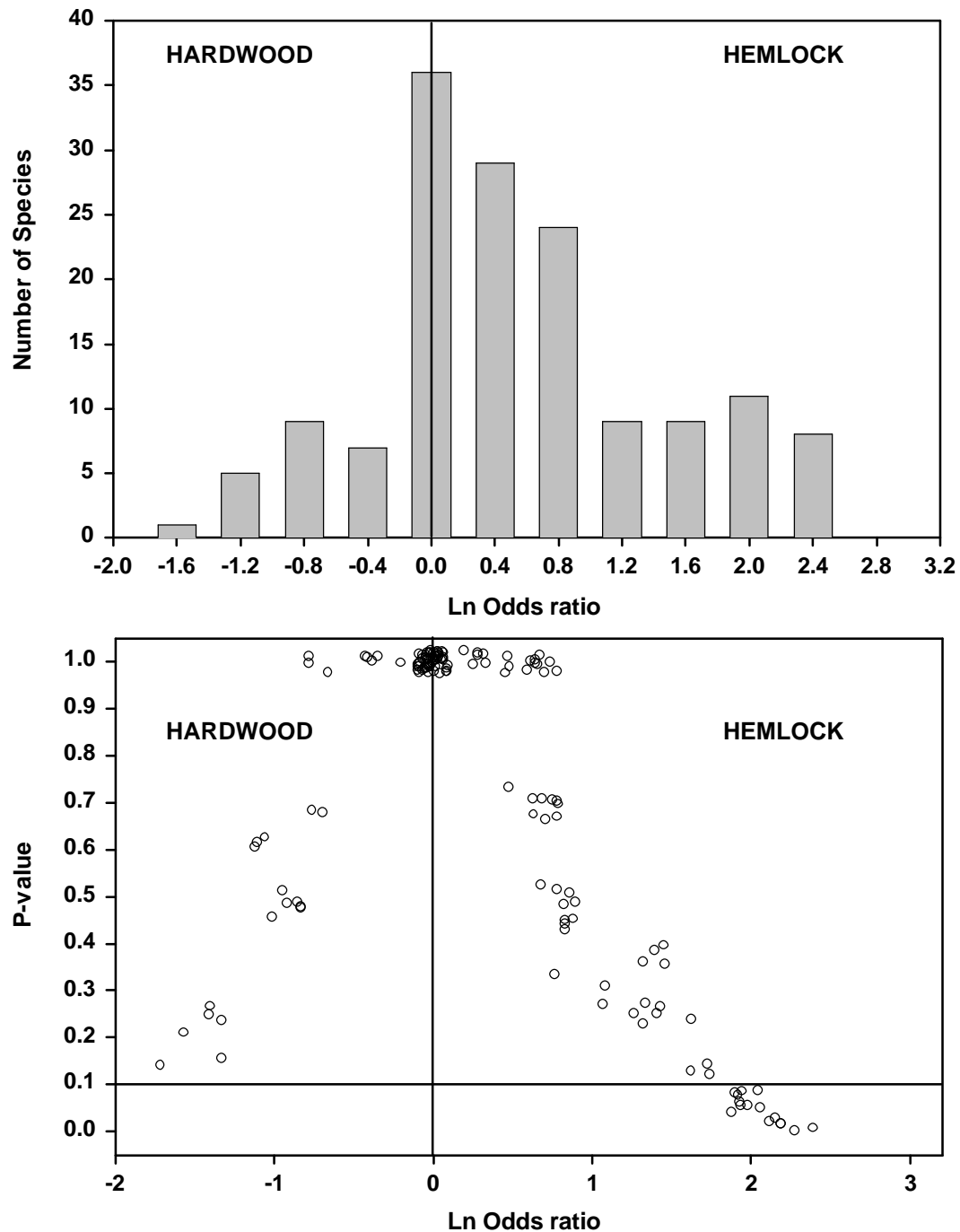


Figure 2-4. Results of odds ratio test to determine taxa-specific associations with vegetation types. For each taxa, ratio of occurrence in streams draining hemlock to that in hardwood was used and therefore positive values indicate a preference for hemlock. Top figure shows the distribution of species with various odds ratios. Bottom figure shows the significance (i.e., p-values) as a function of the odds ratio. A random jitter function was applied to data to enhance visual separation.

Table 2-4. Identity of taxa with forest type preferences. Strong preference defined as p-values of less than 0.1 in odd ratio test (see Methods). Weak preferences defined as p-values less than 0.30. *indicates taxa found only in streams draining hemlock.

Taxon	Taxonomic Class	Trophic Class
<u>Strong Hemlock Assoc.</u>		
<i>Eurylophella sp.</i>	Ephemeroptera	Collector-gatherer
Leptophlebiidae	Ephemeroptera	Collector-gatherer; shredder-detritivore
<i>Lanthus parvulus</i>	Other Insect (Odonata)	Predator-engulfer
<i>Leuctra sp.</i>	Plecoptera	Shredder-detritivore
Perlidae	Plecoptera	Predator-engulfer
* <i>Hydropsyche ventura</i>	Trichoptera	Collector-filterer
<i>Lepidostoma sp.</i>	Trichoptera	Shredder-detritivore
* <i>Polycentropus sp.</i>	Trichoptera	Predator-engulfer, collector-filterer
<i>Bezzia sp.</i>	Other Insect (Diptera)	Predator-engulfer
<i>Brillia sp.</i>	Midge	Shredder-chewer, collector-gatherer
* <i>Natarsia sp.</i>	Midge	Predator-engulfer
<i>Polypedilum sp.</i>	Midge	Collector-gatherer; predator-engulfer
<i>Rheocricotopus sp.</i>	Midge	Collector-gatherer; shredder-detritivore
<i>Hexatoma sp.</i>	Other Insect (Diptera)	Predator-engulfer
<i>Pseudolimnophila sp.</i>	Other Insect (Diptera)	Predator-engulfer
<u>Weak Hemlock Assoc.</u>		
<i>Adicropheps hitchcocki</i>	Trichoptera	Shredder-detritivore
Limnephilidae	Trichoptera	Shredder-detritivore
<i>Rhyacophila minora</i>	Trichoptera	Predator-engulfer
<i>Promoresia sp.</i>	Other Insect (Coleoptera)	Scraper
<i>Georthocladium sp.</i>	Midge	Collector-gatherer
<i>Psilometriocnemus sp.</i>	Midge	Collector-gatherer
<i>Symbiocladius sp.</i>	Midge	Collector-gatherer
Dolichopodidae	Other Insect (Diptera)	Predator-engulfer
<i>Molophilus sp.</i>	Other Insect (Diptera)	Collector-gatherer
<i>Pisidium sp.</i>	Non-insect (Mollusca)	Scraper
<u>Weak Hardwood Assoc.</u>		
<i>Allocapnia sp.</i>	Plecoptera	Shredder-detritivore
<i>Prostoia similis</i>	Plecoptera	Shredder-detritivore
<i>Chaetocladius sp.</i>	Midge	Collector-gatherer
<i>Diplocladius sp.</i>	Midge	Collector-gatherer
<i>Clinocera sp.</i>	Other Insect (Diptera)	Predator-engulfer
<i>Tipula sp.</i>	Other Insect (Diptera)	Shredder-detritivore

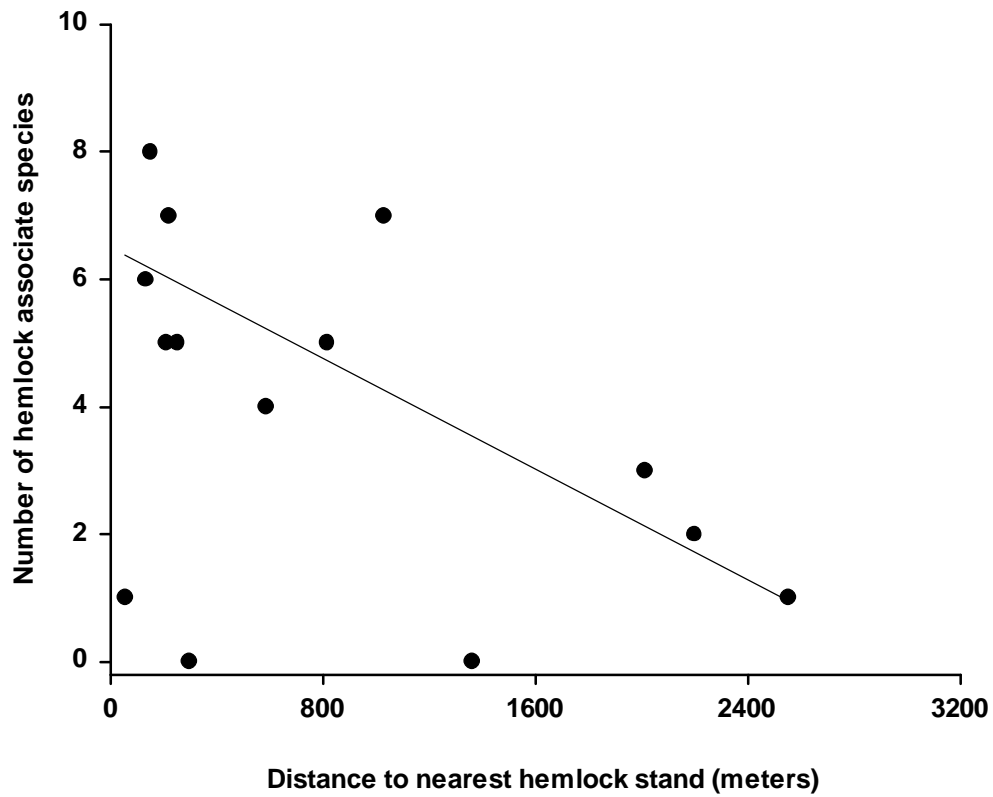


Figure 2-5. Relationship between the number of strong hemlock associates observed in streams draining hardwood forests, as a function of distance to the nearest hemlock stand. Regression line fitted using Robust Regression (Ryan 1997) which reduces the influence of outliers.

Finally, we compared the trophic and taxonomic composition of the 25 hemlock associates (strong and weak) described above to the rest of the community to see whether they represented a random subset of the community or if they were taxonomically or functionally different. We found taxa in the hemlock associate group to be distributed differently among the seven trophic groups (Fishers Exact Test, $\chi^2=9.68$, $p=0.09$) than taxa in the rest of the community. More specifically, we found a significantly larger fraction of predator-engulfer taxa and a significantly smaller fraction of scraper taxa in the hemlock associate group (Fig. 2-6). The pattern was even more pronounced if only strong hemlock associates were included. Also, the proportion of collector-gatherer taxa were marginally lower and the proportion of shredder-detritivore were marginally higher in the hemlock associate group. We observed no differences in composition among the six taxonomic groups (Fishers Exact Test, $\chi^2=2.60$, $p=0.78$), though results for Trichoptera were marginal (Fig. 2-6).

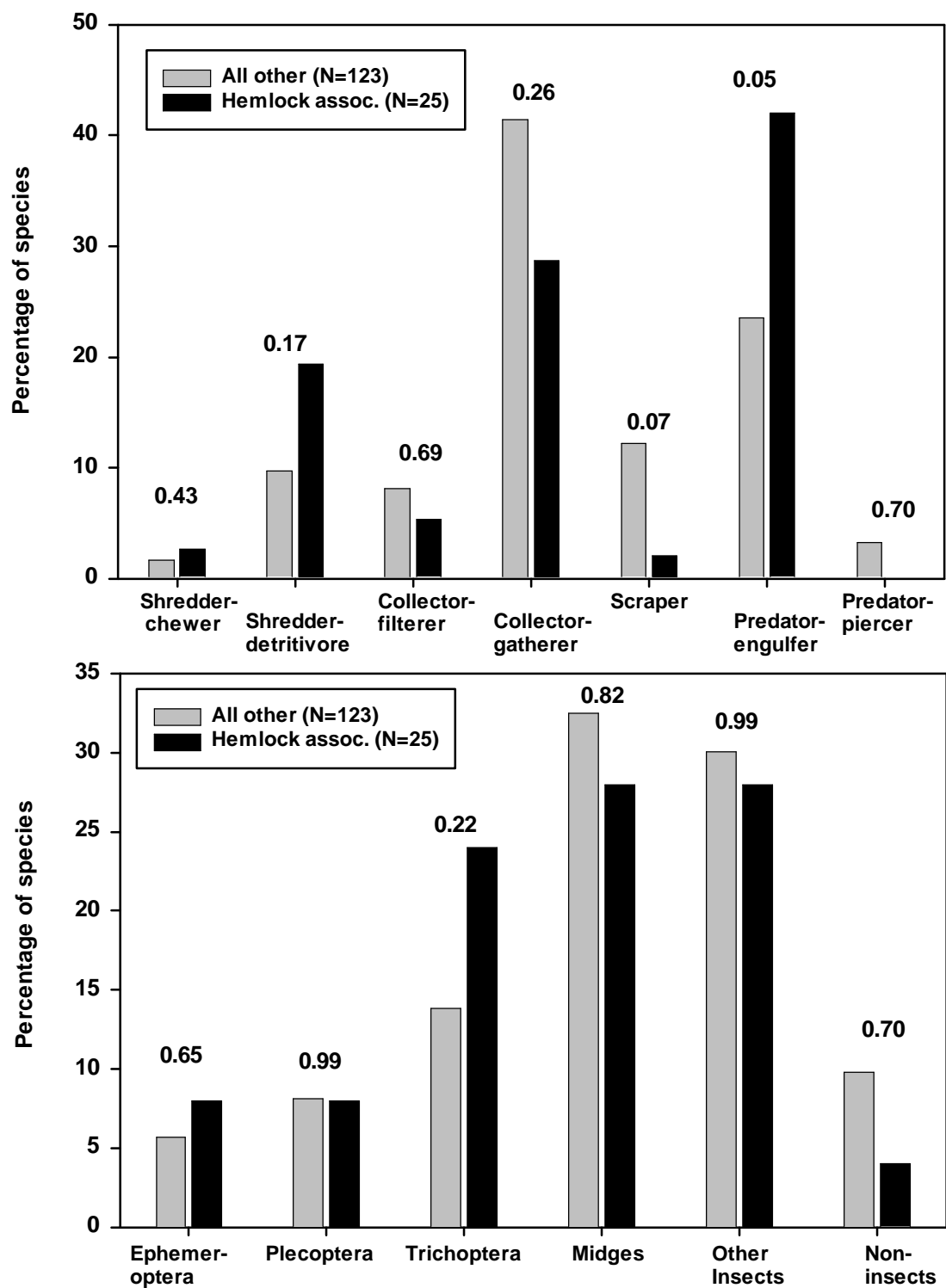


Figure 2-6. Comparison of trophic (top) and taxonomic (bottom) composition between the 25 hemlock associates and the 123 other taxa. Numbers at the top of each pair of bars are p-values resulting from a series of 2X2 Fisher's Exact Tests that test for differences between forest types for each trophic and taxonomic group. Results of the overall contingency tests on the distribution of trophic and taxonomic composition between vegetation types are reported in the text.

DISCUSSION

We found significant differences in all four invertebrate community structure metrics examined between streams draining hemlock and those draining hardwood forests for most stream types. Taxa richness and diversity were higher in hemlock while total density and rarity were lower. First order, mid-slope sites deviated from this pattern for all metrics examined (Fig. 2-1). We believe the steep slope associated with this stream type (Fig. 1-3) reduced residence time of water and nutrients within any particular reach of stream and consequently reduced the time with which forest influences could act. Streams in ravine environments also had steep slopes (Fig. 1-3), but were characterized by a more stair-step profile, with relatively long, low-gradient reaches punctuated by large waterfalls. Consequently, residence time of water and nutrients in ravines may be longer. Geomorphic characteristics including slope and valley shape have long been known to influence biological structure of stream communities and their responses to disturbance (Naiman et al. 1992), and they are the basis for most contemporary stream classification systems (e.g., Rosgen 1985, Frissel et al. 1986, Hawkins et al. 1993).

In addition, we found about 10% (N=15) of all invertebrate taxa collected occurred significantly more often in streams draining hemlock (Fig. 2-4), and that these hemlock associates were not a random subset of the community, but rather had a trophic composition distinct from the rest of the community (Fig. 2-6). Specifically, the proportion of predators was higher and the proportion of grazing algivores was lower in "hemlock associates" than the rest of the community. An additional 7% (N=10) showed a weaker preference for hemlock. Furthermore, these taxa showed a relatively strong association with hemlock even where they occurred in streams draining hardwood forests (Fig. 2-5). Specifically, the number of "strong hemlock associates" in hardwood sites correlated with the proximity of those streams to hemlock stands. Two streams draining hardwood had few or no hemlock associates despite their relative proximity to hemlock (Fig. 2-5). This suggests that, in addition to proximity to hemlock stands, other factors such as the size of the nearest hemlock stand, the number of hemlock stands nearby, the amount of stream habitat within hemlock stands, and/or stochastic factors related to dispersal and distribution may also be important. Nevertheless, the fact that there were no sites distant from hemlock stands that supported large number of "hemlock associates" further supports the argument that hemlock, or stream conditions induced by hemlock, are important to these species. This pattern is consistent with a source-sink model whereby individuals frequently disperse from hemlock sites to hardwood sites, but the survival and/or reproductive capacity of these immigrants is compromised. Thus, despite the occurrence of many of these taxa in hardwood sites, habitat conditions in streams draining hardwood forests may not be sufficient to sustain these taxa over the long term in the absence of hemlock. Dispersal patterns of aquatic insects are poorly understood and the relationship of aquatic insect dispersal with productivity, disturbance patterns, and habitat conditions has not been determined for most taxa (Sheldon 1984). Vegetation-induced differences in stream habitat conditions that cause the biological differences we observed will be explored in Chapter 4.

Whatever the proximate cause, it is clear that streams draining hemlock forests represent "hot spots" of diversity within DEWA. If the distribution and abundance of hemlock forests are compromised by HWA, we would predict a significant decline in both alpha (within site) and gamma (park-wide) aquatic invertebrate diversity. Declines in invertebrate diversity might also be expected to cascade to other assemblages, both aquatic (e.g., fish) and terrestrial (e.g., insectivorous birds and mammals), throughout the watershed.

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Appendix 2-A. List of taxa positively identified from DEWA samples and their respective trophic classification. Trophic classes were derived from Merrit and Cummins (1996) and are as follows: SC=shredder-chewer; SD=shredder-detritivore; SG=shredder-gouger; CF=collector-filterer; CG=collector-gatherer; S=scrapper; MP=macrophyte piercer; PE=predator-engulfer; PP=predator-piercer; and PA=parasites.

Phylum	Class	Order	Family	Genus/Species	Trophic
Annelida	Oligochaeta	Haplotaxida	Megascolecidae		CG
Annelida	Oligochaeta	Lumbricida	Lumbricidae		CG
Annelida	Oligochaeta	Lumbriculida	Lumbriculidae	Lumbriculus variegatus	CG
Annelida	Oligochaeta	Tubificida	Enchytraeidae		CG
Annelida	Oligochaeta	Tubificida	Tubificidae	Spirosperma nikolskyi	CG
Arthropoda	Arachnida	Acariformes	Hydryphantidae		PE,PA
Arthropoda	Arachnida	Acariformes	Torrenicolidae	Torrenicola sp.	PE,PA
Arthropoda	Crustacea	Amphipoda	Crangonyctidae	Stegonectes sp.	CG,SD,PE
Arthropoda	Crustacea	Decapoda	Cambaridae		CG,SD,PE
Arthropoda	Insecta	Collembola	Hypogastruridae	Xynella sp.	CG
Arthropoda	Insecta	Collembola	Isotomidae	Agrenia sp.	CG
Arthropoda	Insecta	Ephemeroptera	Ameletidae	Ameletus sp.	S,CG
Arthropoda	Insecta	Ephemeroptera	Baetidae	Acerpenna pygmaea	CG
Arthropoda	Insecta	Ephemeroptera	Baetidae	Baetis tricaudatus	CG,S
Arthropoda	Insecta	Ephemeroptera	Baetidae	Baetis sp. (two-tail)	CG,S
Arthropoda	Insecta	Ephemeroptera	Ephemerellidae	Ephemerella dorothea	CG,S
Arthropoda	Insecta	Ephemeroptera	Ephemerellidae	Ephemerella rotunda	CG,S
Arthropoda	Insecta	Ephemeroptera	Ephemerellidae	Eurylophella funeralis	CG
Arthropoda	Insecta	Ephemeroptera	Heptageniidae	Epeorus (Iron) sp.	CG,S
Arthropoda	Insecta	Ephemeroptera	Heptageniidae	Rhithrogena sp.	CG,S
Arthropoda	Insecta	Ephemeroptera	Heptageniidae	Stenonema merivulvum	CG,S
Arthropoda	Insecta	Ephemeroptera	Heptageniidae	Stenonema pudicum	CG,S
Arthropoda	Insecta	Ephemeroptera	Heptageniidae	Stenonema vicarium	CG,S
Arthropoda	Insecta	Ephemeroptera	Isonychiidae	Isonychia sp.	CF
Arthropoda	Insecta	Ephemeroptera	Leptophlebiidae	Paraleptophlebia sp.	CG,SD
Arthropoda	Insecta	Odonata	Aeschnidae	Boyeria vinosa	PE
Arthropoda	Insecta	Odonata	Coenagrionidae	Ischnura sp.	PE
Arthropoda	Insecta	Odonata	Cordulegasteridae	Cordulegaster sp.	PE
Arthropoda	Insecta	Odonata	Gomphidae	Lanthus parvulus	PE
Arthropoda	Insecta	Plecoptera	Capniidae	Allocapnia sp.	SD
Arthropoda	Insecta	Plecoptera	Capniidae	Paracapnia sp.	SD
Arthropoda	Insecta	Plecoptera	Chloroperlidae	Sweltsa sp.	PE
Arthropoda	Insecta	Plecoptera	Leuctridae	Leuctra sibleyi	SD
Arthropoda	Insecta	Plecoptera	Nemouridae	Amphinemura delosa	SD
Arthropoda	Insecta	Plecoptera	Nemouridae	Amphinemura wui	SD
Arthropoda	Insecta	Plecoptera	Nemouridae	Paranemoura perfecta	SD
Arthropoda	Insecta	Plecoptera	Nemouridae	Prostoia similis	SD
Arthropoda	Insecta	Plecoptera	Peltoperlidae	Tallaperla sp.	SD
Arthropoda	Insecta	Plecoptera	Perlidae	Agnetina capitata	PE
Arthropoda	Insecta	Plecoptera	Perlidae	Acroneuria abnormis	PE
Arthropoda	Insecta	Plecoptera	Perlidae	Acroneuria carolinensis	PE

Appendix 2-A (continued).

Phylum	Class	Order	Family	Genus/Species	Trophic
Arthropoda	Insecta	Plecoptera	Perlodidae	Malirekus iroquois	PE
Arthropoda	Insecta	Plecoptera	Pteronarcyidae	Pteronarcys biloba	SD
Arthropoda	Insecta	Plecoptera	Pteronarcyidae	Pteronarcys proteus	SD
Arthropoda	Insecta	Plecoptera	Taeniopterygidae	Bolotoperla rossi	SD
Arthropoda	Insecta	Plecoptera	Taeniopterygidae	Oemopteryx contorta	SD
Arthropoda	Insecta	Hemiptera	Corixidae	Hesperocorixa sp.	MP
Arthropoda	Insecta	Megaloptera	Corydalidae	Nigronia fasciatus	PE
Arthropoda	Insecta	Megaloptera	Corydalidae	Nigronia serricornis	PE
Arthropoda	Insecta	Megaloptera	Sialidae	Sialis sp.	PE
Arthropoda	Insecta	Trichoptera	Brachycentridae	Adicrophleps hitchcocki	SD
Arthropoda	Insecta	Trichoptera	Brachycentridae	Micrasema sprulesi	SD,SC
Arthropoda	Insecta	Trichoptera	Glossosomatidae	Glossosoma sp.	S
Arthropoda	Insecta	Trichoptera	Hydroptilidae	Palaeagapetus celsus	SD
Arthropoda	Insecta	Trichoptera	Hydroptilidae	Hydroptila sp.	MP,S
Arthropoda	Insecta	Trichoptera	Hydropsychidae	Cheumatopsyche sp.	CF
Arthropoda	Insecta	Trichoptera	Hydropsychidae	Diplectrona modesta	CF
Arthropoda	Insecta	Trichoptera	Hydropsychidae	Hydropsyche sparna	CF
Arthropoda	Insecta	Trichoptera	Hydropsychidae	Hydropsyche ventura	CF
Arthropoda	Insecta	Trichoptera	Hydropsychidae	Parapsyche apicalis	CF
Arthropoda	Insecta	Trichoptera	Lepidostomatidae	Lepidostoma sp.	SD
Arthropoda	Insecta	Trichoptera	Limnephilidae	Ironoquia sp.	SD
Arthropoda	Insecta	Trichoptera	Limnephilidae	Pycnopsyche sp.	SD
Arthropoda	Insecta	Trichoptera	Molannidae	Molanna blenda	S,CG,PE
Arthropoda	Insecta	Trichoptera	Odontoceridae	Psilotreta frontalis	S,CG
Arthropoda	Insecta	Trichoptera	Philopotamidae	Dolophilodes distinctus	CF
Arthropoda	Insecta	Trichoptera	Polycentropodidae	Polycentropus sp.	PE,CF,SD
Arthropoda	Insecta	Trichoptera	Psychomyiidae	Lype diversa	S
Arthropoda	Insecta	Trichoptera	Rhyacophilidae	Rhyacophila fuscula	PE
Arthropoda	Insecta	Trichoptera	Rhyacophilidae	Rhyacophila glaberrima	PE
Arthropoda	Insecta	Trichoptera	Rhyacophilidae	Rhyacophila minora	PE
Arthropoda	Insecta	Trichoptera	Rhyacophilidae	Rhyacophila nigrita	PE
Arthropoda	Insecta	Trichoptera	Rhyacophilidae	Rhyacophila torva	PE
Arthropoda	Insecta	Trichoptera	Uenoidae	Neophylax concinnu	S
Arthropoda	Insecta	Trichoptera	Uenoidae	Neophylax nacatu	S
Arthropoda	Insecta	Lepidoptera			SD,S
Arthropoda	Insecta	Coleoptera	Curculionidae		SC
Arthropoda	Insecta	Coleoptera	Dryopidae	Helichus sp.	SD
Arthropoda	Insecta	Coleoptera	Elateridae	Megapenthes sp.	CG
Arthropoda	Insecta	Coleoptera	Elmidae	Macronychus glabratus	CG
Arthropoda	Insecta	Coleoptera	Elmidae	Oulimnius latiusculus	CG,S
Arthropoda	Insecta	Coleoptera	Elmidae	Promoresia tardella	CG,S
Arthropoda	Insecta	Coleoptera	Halipidae	Peltodytes lengi	PP,SD,PE

Appendix 2-A (continued).

Phylum	Class	Order	Family	Genus/Species	Trophic
Arthropoda	Insecta	Coleoptera	Psephenidae	Ectopria nervosa	S
Arthropoda	Insecta	Coleoptera	Psephenidae	Psephenus herricki	S
Arthropoda	Insecta	Diptera	Blephariceridae	Blepharicera sp.	S
Arthropoda	Insecta	Diptera	Ceratopogonidae	Bezzia/Palpomyia sp.	PE
Arthropoda	Insecta	Diptera	Ceratopogonidae	Ceratopogon sp.	PE
Arthropoda	Insecta	Diptera	Ceratopogonidae	Probezzia sp.	PE
Arthropoda	Insecta	Diptera	Chironomidae	Brillia flavifrons	SC,CG
Arthropoda	Insecta	Diptera	Chironomidae	Brillia parva	SC,CG
Arthropoda	Insecta	Diptera	Chironomidae	Brillia sera	SC,CG
Arthropoda	Insecta	Diptera	Chironomidae	Brundiniella sp.	PE
Arthropoda	Insecta	Diptera	Chironomidae	Chaetocladius dentiforceps	CG
Arthropoda	Insecta	Diptera	Chironomidae	Chaetocladius piger	CG
Arthropoda	Insecta	Diptera	Chironomidae	Conchapelopia sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Constempellina sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Corynoneura sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Cricotopus bicinctus	SC,CG
Arthropoda	Insecta	Diptera	Chironomidae	Diamesa sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Diplocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Doithrix sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Eukiefferiella brehmi	CG,S,PE
Arthropoda	Insecta	Diptera	Chironomidae	Eukiefferiella brevicar	CG,S,PE
Arthropoda	Insecta	Diptera	Chironomidae	Eukiefferiella claripennis	CG,S,PE
Arthropoda	Insecta	Diptera	Chironomidae	Eukiefferiella devonica	CG,S,PE
Arthropoda	Insecta	Diptera	Chironomidae	Eukiefferiella gracei	CG,S,PE
Arthropoda	Insecta	Diptera	Chironomidae	Eukiefferiella pseudomontana	CG,S,PE
Arthropoda	Insecta	Diptera	Chironomidae	Eukiefferiella rectangularis	CG,S,PE
Arthropoda	Insecta	Diptera	Chironomidae	Georthocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Heleniella sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Heterotrissocladius hirtapex	CG
Arthropoda	Insecta	Diptera	Chironomidae	Hydrobaenus sp.	S,CG
Arthropoda	Insecta	Diptera	Chironomidae	Limnophyes sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Larsia sp.	PE
Arthropoda	Insecta	Diptera	Chironomidae	Meropelopia sp.	PE
Arthropoda	Insecta	Diptera	Chironomidae	Micropsectra sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Microtendipes pedellus	CF
Arthropoda	Insecta	Diptera	Chironomidae	Nanocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Natarsia baltimorea	PE
Arthropoda	Insecta	Diptera	Chironomidae	Orthocladius clarkei	CG
Arthropoda	Insecta	Diptera	Chironomidae	Orthocladius dorens	CG
Arthropoda	Insecta	Diptera	Chironomidae	Orthocladius mallochii	CG
Arthropoda	Insecta	Diptera	Chironomidae	Orthocladius obumbratus	CG
Arthropoda	Insecta	Diptera	Chironomidae	Parametrioctenus sp.	CG

Appendix 2-A (continued).

Phylum	Class	Order	Family	Genus/Species	Trophic
Arthropoda	Insecta	Diptera	Chironomidae	Paratendipes sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Paratrichocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Polypedilum aviceps	SC,CG,PE
Arthropoda	Insecta	Diptera	Chironomidae	Polypedilum illinoense	SC,CG,PE
Arthropoda	Insecta	Diptera	Chironomidae	Polypedilum tritum	SC,CG,PE
Arthropoda	Insecta	Diptera	Chironomidae	Pseudorthocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Pseudosmittia sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Psilometriocnemus sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Rheocricotopus eminellobus	CG,SC,PE
Arthropoda	Insecta	Diptera	Chironomidae	Rheocricotopus tuberculatus	CG,SC,PE
Arthropoda	Insecta	Diptera	Chironomidae	Rheopelopia sp.	PE
Arthropoda	Insecta	Diptera	Chironomidae	Rheosmittia sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Rheotanytarsus sp.	CF
Arthropoda	Insecta	Diptera	Chironomidae	Stempellina sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Stempellinella sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Stenochironomus sp.	CG,SG
Arthropoda	Insecta	Diptera	Chironomidae	Stilocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Synorthocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Tanytarsus sp.	CF
Arthropoda	Insecta	Diptera	Chironomidae	Thienemanniella sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Tribelos jucundus	CG
Arthropoda	Insecta	Diptera	Chironomidae	Trissocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Trissocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Tvetenia bavarica	CG
Arthropoda	Insecta	Diptera	Chironomidae	Zavrelimyia sp.	PE
Arthropoda	Insecta	Diptera	Dixidae	Dixa sp.	CG
Arthropoda	Insecta	Diptera	Dolichopodidae	Medetera sp.	PE
Arthropoda	Insecta	Diptera	Empididae	Chelifera sp.	PE
Arthropoda	Insecta	Diptera	Empididae	Clinocera sp.	PE
Arthropoda	Insecta	Diptera	Empididae	Oreogeton sp.	PE
Arthropoda	Insecta	Diptera	Rhagionidae	Chrysopilus sp.	PP
Arthropoda	Insecta	Diptera	Sciaridae	Corynoptera sp.	CG
Arthropoda	Insecta	Diptera	Simuliidae	Prosimulium arvum	CF
Arthropoda	Insecta	Diptera	Simuliidae	Stegopterna mutata	CF
Arthropoda	Insecta	Diptera	Simuliidae	Simulium vittatum	CF
Arthropoda	Insecta	Diptera	Stratiomyidae		CG
Arthropoda	Insecta	Diptera	Tabanidae	Chrysops sp.	PP
Arthropoda	Insecta	Diptera	Tabanidae	Tabanus sp.	PP
Arthropoda	Insecta	Diptera	Tipulidae	Antocha sp.	SD
Arthropoda	Insecta	Diptera	Tipulidae	Dicranota sp.	PE
Arthropoda	Insecta	Diptera	Tipulidae	Erioptera sp.	CG
Arthropoda	Insecta	Diptera	Tipulidae	Hexatoma sp.	PE

Appendix 2-A (continued).

Phylum	Class	Order	Family	Genus/Species	Trophic
Arthropoda	Insecta	Diptera	Tipulidae	Pedicia sp.	PE
Arthropoda	Insecta	Diptera	Tipulidae	Pilaria sp.	PE
Arthropoda	Insecta	Diptera	Tipulidae	Pseudolimnophila sp.	PE,SD
Arthropoda	Insecta	Diptera	Tipulidae	Tipula sp.	SD
Arthropoda	Insecta	Diptera	Syrphidae		CG
Mollusca	Gastropoda	Basommatophora	Planorbidae	Gyraulus parvus	S
Mollusca	Gastropoda	Basommatophora	Physidae	Physella sp.	S
Mollusca	Pelecypoda	Eulamellibranchia	Sphaeriidae	Pisidium casertanum	CG

Chapter 3: Influence of eastern hemlock (*Tsuga canadensis*) on fish community structure in small headwater streams of the Delaware Water Gap National Recreation Area.

Robert M. Ross and Randy M. Bennett

INTRODUCTION

This report summarizes findings of the USGS Biological Resources Division work on fish biodiversity in eastern hemlock (*Tsuga canadensis*) stands of the Delaware Water Gap National Recreation Area (DEWA). Parallel studies of macroinvertebrate biodiversity are reported elsewhere. This report addresses objective two (determine the contribution of hemlock stands to aquatic biodiversity in DEWA) of the Leetown Science Center study plan, entitled "Aquatic Biodiversity in Eastern Hemlock Forests."

METHODS

We initially planned to incorporate the blocked-pair design described in Chapter 1. However, a large fraction of the selected streams dried up during the summer fish sampling period (Table 1), and consequently our sampling was compromised and we were only able to employ the paired approach in our analysis for a subset of selected site pairs. Specifically, of the 28 stream reaches initially selected (Chapter 1), only 13 contained sufficient flow to support fish. Four streams were completely dry and seven were mostly dry (Table 1). Ultimately, we sampled the 24 stream reaches that contained water.

Electrofishing techniques were used to collect fish in single passes, downstream to upstream. Collected individuals were identified, measured to the nearest mm of total length, and released behind the advancing electroshocker. Species, functional, and tolerance diversities were calculated for each stream using the Shannon-Wiener diversity index, H' . For functional and tolerance diversity analyses, fish species were assigned commonly accepted trophic levels (piscivore, insectivore, or omnivore) and tolerance levels (intolerant, tolerant, or other [either intermediate in tolerance or conflicting designations in the literature]) prior to index computation by stream sample. Using the stratified-pair design described in Chapter 1, diversity indices for each stream were subtracted from those of its pair (hardwood vs hemlock). The remaining 14 means were averaged and the result compared to zero. The null hypothesis of no significant difference in means was rejected if $p < 0.10$. Fisher's Exact Test was used on unstratified presence/absence data to test for species, functional, and tolerance associations among stand type, terrain type, and order. Proportions and frequencies were also calculated for the stand types (hardwood or hemlock), terrain types (bench, ravine, or slope), and stream orders (1st or 2nd).

Table 1. Extent of drying for the 28 streams sampled in DEWA. Wet=entire stream channel wetted; mostly wet=>50% of stream channel wetted; mostly dry=<50% of stream channel wetted; and dry=completely dry.

Site #	Stand#	Forest type	Terrain	Stream order	Extent of drying	Fish
042201	142	hardwood	ravine	2	wet	present
051101	243	hardwood	bench	1	mostly dry	present
072113	365	hemlock	ravine	1	wet	present
081102	529	hardwood	bench	1	dry	absent
083102	561	hardwood	slope	1	dry	absent
092112	485	hemlock	ravine	1	mostly dry	absent
102211	657	hemlock	ravine	2	wet	present
111113	822	hemlock	bench	1	wet	absent
152102	1020	hardwood	ravine	1	mostly dry	absent
152213	1059	hemlock	ravine	2	mostly wet	absent
162101	1202	hardwood	ravine	1	mostly dry	absent
172212	1191	hemlock	ravine	2	wet	present
182202	1327	hardwood	ravine	2	wet	present
191202	1335	hardwood	bench	2	wet	present
191211	1368	hemlock	bench	2	wet	present
192111	1449	hemlock	ravine	1	wet	present
222103	1784	hardwood	ravine	1	wet	present
232203	1850	hardwood	ravine	2	dry	absent
271103	1909	hardwood	bench	1	dry	absent
271111	1509	hemlock	bench	1	mostly dry	absent
271112	2037	hemlock	bench	1	wet	absent
273103	1614	hardwood	slope	1	mostly dry	absent
273111	1673	hemlock	slope	1	mostly wet	absent
273112	1653	hemlock	slope	1	mostly wet	absent
273113	1742	hemlock	slope	1	wet	present
283101	2204	hardwood	slope	1	mostly dry	absent
291201	2035	hardwood	bench	2	wet	present
291212	2107	hemlock	bench	2	wet	present

RESULTS AND DISCUSSION

Streams which dewatered or partially dewatered were not more likely to be found in a particular stand type (Fisher's Exact Test $p=0.257$). From the streams which were at least partially watered a total of 1,406 fish of 15 species and 7 families were collected. Eight of 13 species (62%) were found only in hardwood sites, while one of seven species (14%; golden shiner) was unique to hemlock stands. Among the six species found in both hardwood and hemlock stands, American eel and creek chub were found in greater proportion in hardwood than hemlock sites, though neither exceeded 8% in either stand type (Table 2). Brook trout and brown trout were three times and twice as prevalent in hemlock as hardwood stands, respectively (Table 2).

Table 2. Proportional sample representation for the six species found in both hardwood (490 fish) and hemlock (832 fish) stands.

Species	No. stands found in		No. fish found in		Proportion of sample	
	Hardwood	Hemlock	Hardwood	Hemlock	Hardwood	Hemlock
American eel	2	1	20	5	0.04	0.01
Brown trout	1	1	22	71	0.04	0.09
Brook trout	1	4	21	107	0.04	0.13
Blacknose dace	4	6	384	637	0.78	0.77
Creek chub	1	1	40	7	0.08	0.01
Pumpkinseed	3	3	3	5	0.01	0.01

When the data were differentiated by terrain type (regardless of stand type), brook trout were found to be the most ubiquitous species, found in bench, ravine, and slope habitats (Table 3). Species found only in benches were golden shiner and creek chub, while those found only in ravines were American eel, brown trout, cutlips minnow, common shiner, longnose dace, and fallfish. Slope habitats had no unique species. There were no unique species in first order streams, which harbored only four species: brook trout, blacknose dace, pumpkinseed, and bluegill.

From an individual stream perspective, with one exception, both hardwood and hemlock stream samples harbored only one to four species of fish. The exception was Shimers Brook, a 2nd-order ravine hardwood stream segment with 12 species, well outside the range for all other streams sampled. Shimers Brook was also the most taxonomically diverse stream, followed by Tumbling Water 2, a 2nd-order bench hemlock site, with four species among only 18 individual fish. Sufficient stream data were available to statistically compare the proportion (after arcsine transformation) of insectivores in samples where fish were present (hardwood versus hemlock). Insectivores were in significantly higher proportion in hardwood (0.90) than in hemlock (0.46) stands ($F_{1,8} = 7.0$, $p = 0.03$). Likewise, hemlock stands had greater proportions of piscivores (0.85 versus 0.54), though not significantly different ($F_{1,5} = 1.26$, $p = 0.62$). Neither the taxa richness metric nor the three diversity metrics showed a significant forest stand-type effect (Fig.1). When analyzed by pooled forest type without regard to other physiographic variables, we found species and tolerance diversities were similar for the two groups, though mean functional diversity for hemlock was numerically twice that of hardwood stands (Table 4). Similar analysis of pooled terrain types showed highest numerical diversities (functional and tolerance) in bench, followed by ravine, and lastly slope terrains, while stream orders showed much higher diversity in 2nd order (Table 4). Mean stream species diversity (H_s) was 0.10 ($n = 14$) for hardwood stands and 0.09 ($n = 14$) for hemlock stands ($F_{1,26} = 0.00$, $p = 0.97$). Mean stream functional diversity (H_f) was 0.04 for hardwood stands and 0.07 for hemlock stands ($F_{1,26} = 0.74$, $p = 0.40$). Tolerance diversity (H_t) was the same for hardwood ($0 = 0.07$) and hemlock ($0 = 0.08$) stands ($F_{1,126} = 0.00$, $p = 0.99$). Using unstratified presence/absence data the only species to show a stand preference was bluegill (Table 3). Blacknose dace, insectivores, and other (tolerance) preferred bench and ravine over midslope terrain. American eel, blacknose dace, pumpkinseed, insectivores, omnivores, tolerant, intolerant, and other were found significantly more often in 2nd order than 1st order.

Table 3. Presence (x) of each species, trophic guild, and tolerance guild in each stand type, terrain type, and stream order with a statistical analysis of association (Fisher Exact Test) using presence/absence data. Abbreviations under trophic guild are omnivore (O), insectivore (I), and piscivore (P); those under tolerance are tolerant (T), intolerant (I), and other (O). In parentheses is the number of sample units for each physiographic variable. Asterisks indicate the class(es) statistically preferred by a species or group.

Common name	Species	Scientific name	guild	Tolerance	Stand found in				Terrain type found in				Stream order found in	
					Hardwood	Hemlock	Fisher p value	Bench	Ravine	Slope	Fisher p value	1	2	Fisher p value
American eel		<u>Anguilla rostrata</u>	I	T	X	X	1.000		X		0.211		X*	0.037
Brown trout		<u>Salmo trutta</u>	P	I	X	X	1.000		X		0.492		X	0.119
Brook trout		<u>Salvelinus fontinalis</u>	P	I	X	X	0.336	X	X	X	1.000	X	X	1.000
Cutlips minnow		<u>Exoglossum maxillingua</u>	I	I	X		1.000		X		1.000		X	0.357
Common shiner		<u>Luxilus comutus</u>	O	O	X		1.000		X		1.000		X	0.357
Golden shiner		<u>Notemigonus crysoleucas</u>	O	T		X	1.000	X			0.571		X	0.357
Blacknose dace		<u>Rhinichthys atratulus</u>	I	O	X	X	1.000	X*	X*		0.097	X	X*	0.011
Longnose dace		<u>Rhinichthys cataractae</u>	I	I	X		1.000		X		1.000		X	0.357
Creek chub		<u>Semotilus atromaculatus</u>	O	T	X	X	1.000	X			0.159		X	0.119
Fallfish		<u>Semotilus corporalis</u>	O	T	X		1.000		X		1.000		X	0.357
White sucker		<u>Catostomus commersoni</u>	O	T	X		1.000		X		1.000		X	0.357

Table 3 (cont).

Species		Stand found in				Terrain type found in				Stream order found in				
Common name	Scientific name	guild	Tolerance	Hardwood	Hemlock	Fisher		Bench	Ravine	Slope	Fisher		Fisher	
						p value	p value				1	2		p value
Margined madtom	<u>Noturus insignis</u>	I	I	X		1.000			X		1.000		X	0.357
Pumpkinseed	<u>Lepomis gibbosus</u>	I	I	X	X	1.000		X	X		0.432		X	0.013
Bluegill	<u>Lepomis macrochirus</u>	I	T	X*		0.098		X	X		0.648		X	0.116
Tessellated darter	<u>Etheostoma olmstedti</u>	I	O	X		1.000			X		1.000		X	0.357
Insectivores				X	X	1.000		X*	X*		0.097		X	0.011
Omnivores				X	X	1.000		X	X	X	0.579		X	0.037
Piscivores				X	X	0.385		X	X	X	0.741		X	0.207
Tolerant				X	X	0.695		X	X		0.432		X	0.013
Intolerant				X	X	0.648		X	X	X	0.682		X	0.097
Other				X	X	1.000		X*	X*	X	0.097		X	0.011

Table 4. Unstratified, summed, fish species richness (R), total individuals sampled (N), species diversity (Hs), functional diversity (Hf), and tolerance diversity (Ht) by forest stand type, terrain type, and stream order.

Physiographic variable	Variable types	R	N	H _s	H _f	H _t
Forest stand type	Hardwood	14	573	0.096	0.036	0.075
	Hemlock	7	832	0.089	0.071	0.075
Terrain type	Bench	6	237	0.118	0.071	0.100
	Ravine	13	1146	0.117	0.064	0.092
	Slope	1	23	0.000	0.000	0.000
Stream order	1	4	138	0.030	0.015	0.030
	2	15	1268	0.206	0.122	0.157

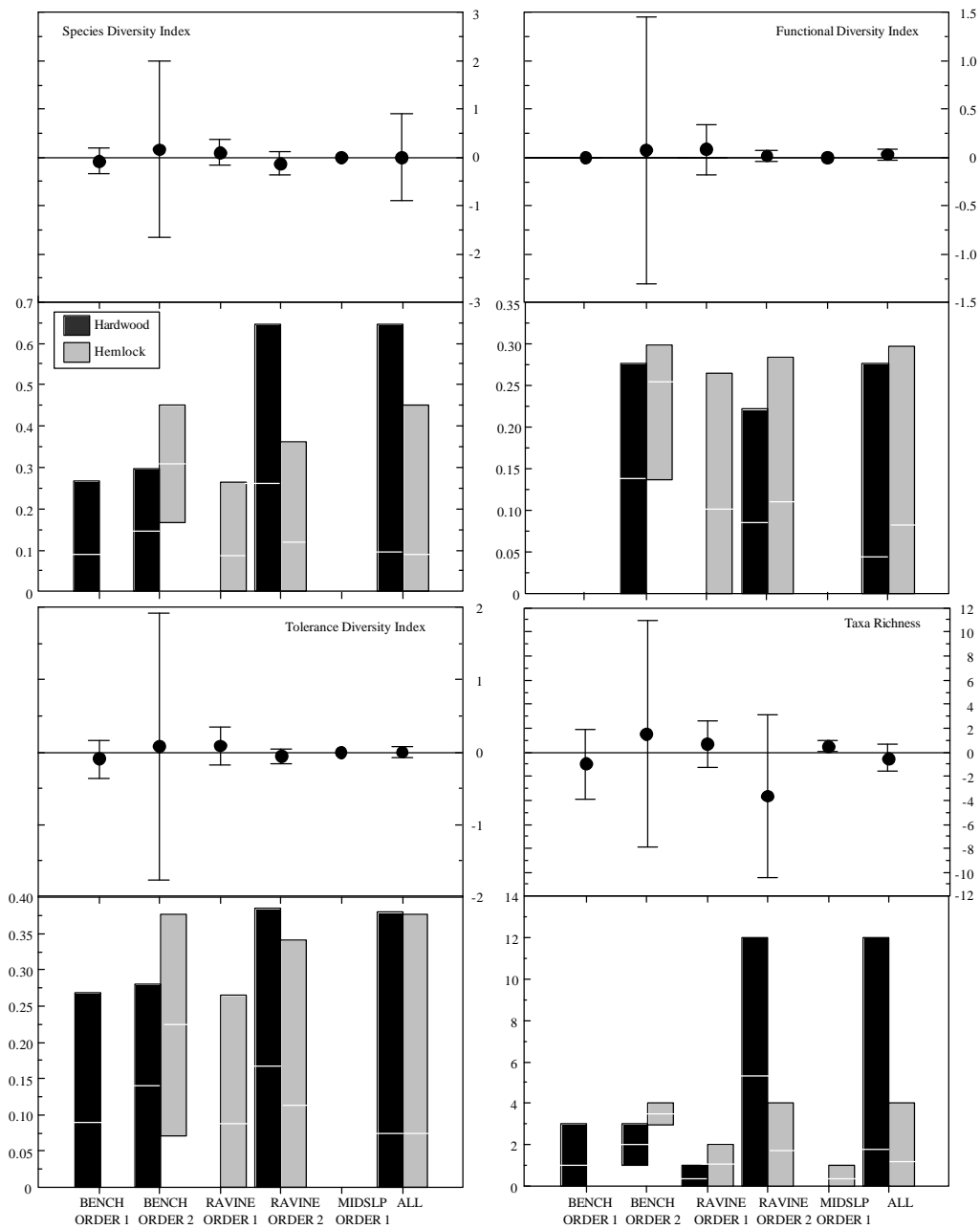


Figure 3-1. Comparison of four community metrics by stand type, terrain type, and stream order. Top graph shows mean differences for stratified pairs. Positive values indicate higher means for hemlock. Bottom panel shows range of values. White line is the mean.

CONCLUSIONS

Fish species associations and other ichthyofaunal qualities unique to hemlock stands were subtle. Both hemlock and hardwood streams typically supported 1 - 4 species of fish. The single golden shiner cannot be considered indicative of hemlock sites. However, brook trout proportions in hemlock were three times those in hardwood stands, and their presence in hemlock versus hardwood streams was four times that of brown trout. Hemlock streams did not differ significantly from hardwood streams in terms of species or tolerance diversity, but functional diversity was twice as high in hemlock as hardwood. Trophic structure was different between the two forest stand types, in that hemlock streams supported proportionally fewer insectivores and more piscivores than hardwood streams. Among terrain types, species found exclusively in or preferring benches were goldenshiner, creek chub, blacknose dace, and bluegill. Species found exclusively in ravines were American eel, brown trout, and four species of minnows. First order streams harbored only brook trout, blacknose dace, and sunfishes, which probably recruited from headwater ponds. Ravines thus appeared to represent for brook trout a transitional terrain, above which it either out-competed or otherwise did not have to compete with its sister salmonid, the brown trout.

Chapter 4. Influence of eastern hemlock (*Tsuga canadensis*) on stream habitat in Delaware Water Gap National Recreation Area and its relationship to biological diversity patterns.

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INTRODUCTION

Biological organization of stream communities is determined in large part by local habitat structure (Southwood 1977). Most aquatic invertebrates and fish species have evolved behavioral and/or morphological adaptations to specific habitat conditions including thermal regimes (e.g., Brandt et al. 1980, Sweeney 1984), substrate sizes (e.g., Minshall 1984, Ross et al. 1987), and flows patterns (Newbury 1984, Coon 1987). Consequently, their occurrence and abundance is highly dependent on availability of preferred habitat conditions. Furthermore, because resources required by aquatic species often vary with season and life cycle stage, the variety and distribution of available habitat types within a stream reach may limit aquatic diversity (Bayley and Li 1996). Finally, the physical conditions within a habitat, and the frequency and magnitude of disturbance events mediate levels of available food resources, and thus constrain competition and predation (Peckarsky and Dodson 1980), thereby indirectly influencing aquatic community structure.

Likewise, local habitat conditions are determined by patterns and processes in the surrounding watershed (Frissel et al. 1986, Poff 1997). Topography, geology, and soils are all important regulators of instream habitat. Of particular importance is the amount and composition of upland and riparian vegetation (see Chapter 2, Introduction section). Consequently, alterations to terrestrial components of the watershed can be expected to have significant consequences to the abundance and distribution of species, and ultimately to the diversity of aquatic assemblages, through their effects on local habitat.

We reported earlier that aquatic invertebrate diversity and brook trout occurrence were significantly higher in streams draining hemlock forests than those draining hardwood forests (Chapters 2 and 3). The purpose of this chapter is to compare local habitat conditions in streams draining hemlock and hardwood forests in an effort to determine the specific mechanism by which hemlock influences biological structure in Delaware Water Gap National Recreation Area.

METHODS

Habitat Sampling

Instream habitat measurements included those for water and the stream channel and were taken within the same stream reaches used to collect fish and macroinvertebrates (Chapters 2 and 3). Water chemistry measurements were taken at each site during spring high-flow conditions (proximate to invertebrate sampling) and summer base-flow conditions (proximate to fish sampling), except temperature which was collected once per hour for an entire year. We were unable to get summer water chemistry measurements for over half of our study sites because they dried up. As a result, we only report spring data. Water chemistry measurements were taken from well-mixed areas within the sample reaches. Water chemistry parameters measured and the instruments used are summarized in Table 4-1.

Table 4-1. Water temperature, water chemistry and hydrology parameters measured in DEWA streams. Type of instruments used and their associated accuracies are also reported.

Parameter	Accuracy	Instrument
Temperature (EC)	±0.02	Onset StowAway temperature logger
Dissolved oxygen (mg/L)	±0.01	Hydrolab Reporter Multi-probe water chemistry meter or Yellow Springs Instruments (YSI) Model 58 Dissolved Oxygen Meter
pH (-log H ⁺ ions)	±0.01	Hydrolab Reporter Multi-probe water chemistry meter
Specific conductance (ms/cm)	±1	Hydrolab Reporter Multi-probe water Chemistry meter or YSI Model 33 S-C-T meter
Turbidity (NTU)	±0.01	LaMotte turbidity meter (Model 2008)
Nutrients (mg/L)		Hatch DR/2000 Direct Reading Spectrophotometer
Total nitrates	±0.01	
Total nitrites	±0.001	
Reactive phosphates	±0.01	
Ammonia	±0.01	
Water Velocity (ft/sec)	±0.01	Marsh-McBirney FloMate model 2000 or model 201D portable flow meters

Temperature was measured hourly between 01 April 1997 and 31 March 1998 at 10 sites (i.e., two replicate site pairs for each of the five different stream types; Fig. 1-6) using Onset temperature loggers (Table 4-1). Two loggers were placed in each stream; one near the bottom of each of the sample reaches where fish and invertebrates were collected, and one between 300 and 1200 meters upstream depending on stream size. Loggers at two sites were lost and so analyses were confined to the remaining eight site pairs.

Stream channel measurements were taken during the period of base flow (July 1997) and included estimates of canopy cover, amount of large woody debris (LWD), and the extent to which streams dried up. Canopy cover (% of stream covered by overhanging vegetation) was measured with a Model A Spherical Densiometer (Forest Densiometers, Bartlesville, OK) at three points within each stream reach (top, middle, and bottom). We counted the number of pieces of large woody debris (LWD) of each of seven size classes (Table 4-2) throughout the entire sample reach. The extent to which streams dried during up during the summer was estimated visually to the nearest 10%. Each stream was subsequently classified into one of four categories based on the amount of stream channel bottom that remained wetted: wet=completely wet; mostly wet=>50% of channel bottom wetted; mostly dry=<50% of channel bottom wetted; and dry=completely dry. Finally, the microhabitat type (Table 2-1, Chapter 2) was recorded at the location where each invertebrate sample was taken. This allowed us to calculate patch richness (i.e., number of different microhabitat types) for each site.

Table 4-2. Classification of large woody debris size classes used to census DEWA streams. Taken from Dolloff et al. (1993).

Class	Diameter (cm)	Length (m)
1	5-10	1-5
2	10-50	1-5
3	>50	1-5
4	5-10	>5
6	>50	>5
7	Root Wad	

Analysis

We compared the differences in most local habitat characteristics between forest types using essentially the same methods as those used to compare invertebrate community structure (Chapter 2). That is, we used general linear modeling to test whether mean differences among site pairs for each response was equal to zero. We compared temperature data to make inferences regarding differences in thermal stability among forest types. Specifically, differences in temperature patterns (means, maxima, minima, and diurnal variation) among site pairs were summarized from hourly temperature data at each site and compared graphically. Finally, We used Fisher's Exact Test to test the hypothesis that streams that dried up were were equally represented between hemlock and hardwood forests. We used StatExact (Mehta and Patel 1997) to calculate Fisher's test statistics and exact p-values.

RESULTS

Water Chemistry and Physical Habitat

Forest type did not have a significant effect on any of the eight water chemistry variables for any single stream type (Fig. 4-1). Since mean differences in water chemistry between forest types were not different among stream types (ANOVA, $p > 0.27$ for all eight variables), we pooled differences across stream types. Overall, dissolved oxygen was higher, and specific conductance, turbidity, and total nitrites were lower in streams draining hemlock forests than those draining hardwood (Fig. 4-1, pooled).

With respect to the stream channel, we found microhabitat patch richness (i.e., numbers of different microhabitat types) was higher in streams draining hemlock for most stream types (Fig. 4-2). However, like invertebrate species richness and Shannon diversity index described earlier (see Chapter 2), the pattern shown by 1st order, mid-slope sites deviated substantially from those of the other stream types. Mean differences in microhabitat richness were not different among stream types when 1st order mid-slope sites were excluded (ANOVA, $F = 1.029$, $p = 0.436$). However, microhabitat differences were significantly different between forest types when mid-slope sites were included ($F = 3.007$, $p = 0.078$). Results from data pooled across all stream types except 1st order mid-slope sites suggest a significant forest type effect on stream microhabitat diversity except in 1st order, mid-slope sites. However, higher microhabitat patch richness observed in streams draining hemlock was not associated with any particular microhabitat types. That is, of the 30 microhabitat types represented in DEWA streams (Table 2-1), none were found to be significantly more common in streams draining hemlock (Results of 2X2 Fishers Exact Tests > 0.2 for all habitat types).

In contrast, we found no overall differences in large woody debris (LWD) or percent canopy cover in streams draining hemlock and mixed hardwood forest types. We observed no significant differences in LWD density (i.e., number of pieces per 100 m stream length) of any of the seven size classes between forest type, or between terrain type and stream order (Multi-response Permutation Procedures, $p > 0.25$ for all three design variables). Likewise, canopy cover was not significantly different between streams draining hemlock and hardwood forest types. However, these measurements were only taken during mid-summer leaf-on. Clearly the deciduous watersheds would contribute substantially less canopy cover during winter leaf-off, and it is very likely that percent cover would be greater in streams draining hemlock if measurements were integrated over the entire year.

Thermal Patterns

We observed a significant forest type effect on thermal patterns at several of our sampling sites. Specifically, median daily temperature tended to be cooler in the summer, warmer in the winter, and less variable throughout the year at study sites draining hemlock forests (Fig. 4-3). However, the pattern described above was not consistent, occurring at only four of eight site pairs where temperature patterns were measured. As with biological differences, the two mid-slope site pairs showed essentially the opposite pattern, and no differences were observed between forest types for two other site pairs (Fig. 4-3).

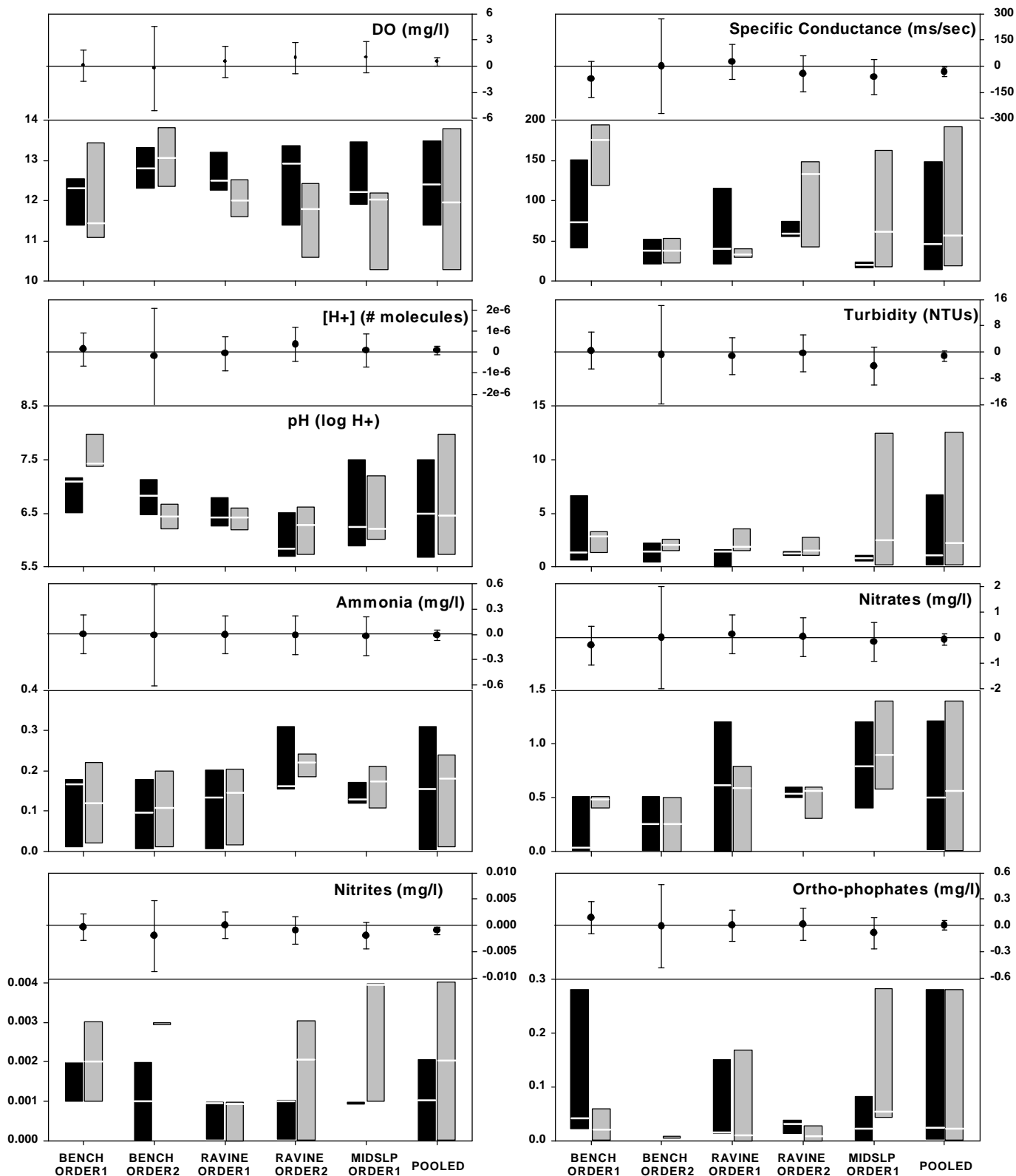


Figure 4-1. Comparison of eight water chemistry variables between streams draining hemlock and hardwood forest types. Top panel shows mean differences (+/- 90% C.L.) between hemlock-hardwood site pairs. Positive values indicate higher means for hemlock. Bottom panel compares the range of values (limits of box) and medians (white lines) between forest types (hemlock=black bars). Comparisons are made within each stream type as well as pooled across stream types (ALL).

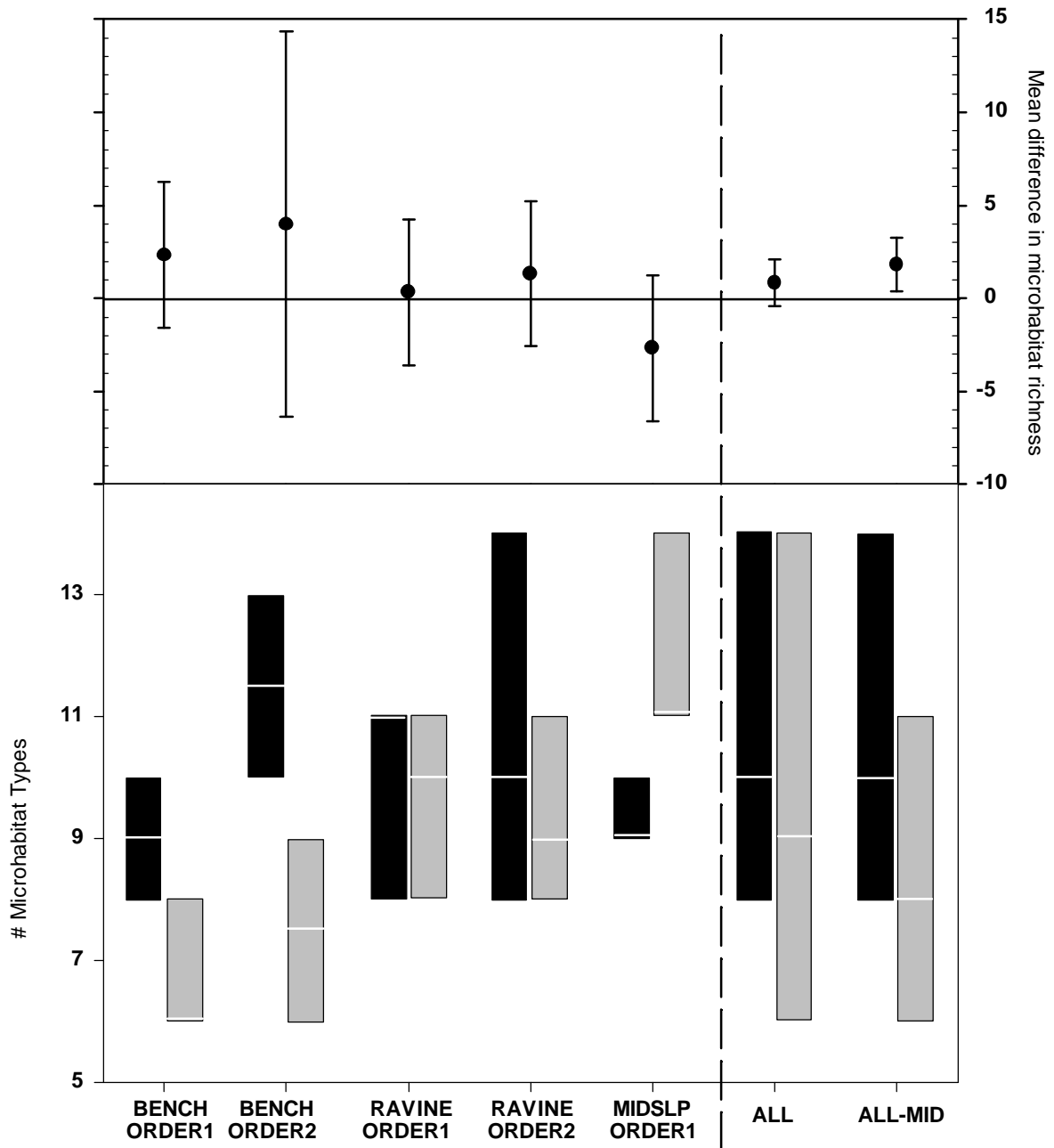


Figure 4-2. Comparison of microhabitat patch richness between streams draining hemlock and hardwood forests. Top panel shows mean differences (\pm 90% C.L.) between hemlock-hardwood site pairs. Positive values indicate higher means for hemlock. Bottom panel compares the range of values (limits of box) and medians (white line) between forest types (hemlock=black bars). Comparisons are made within each stream type as well as pooled across stream types (ALL) and all but midslope sites (ALL-MID).

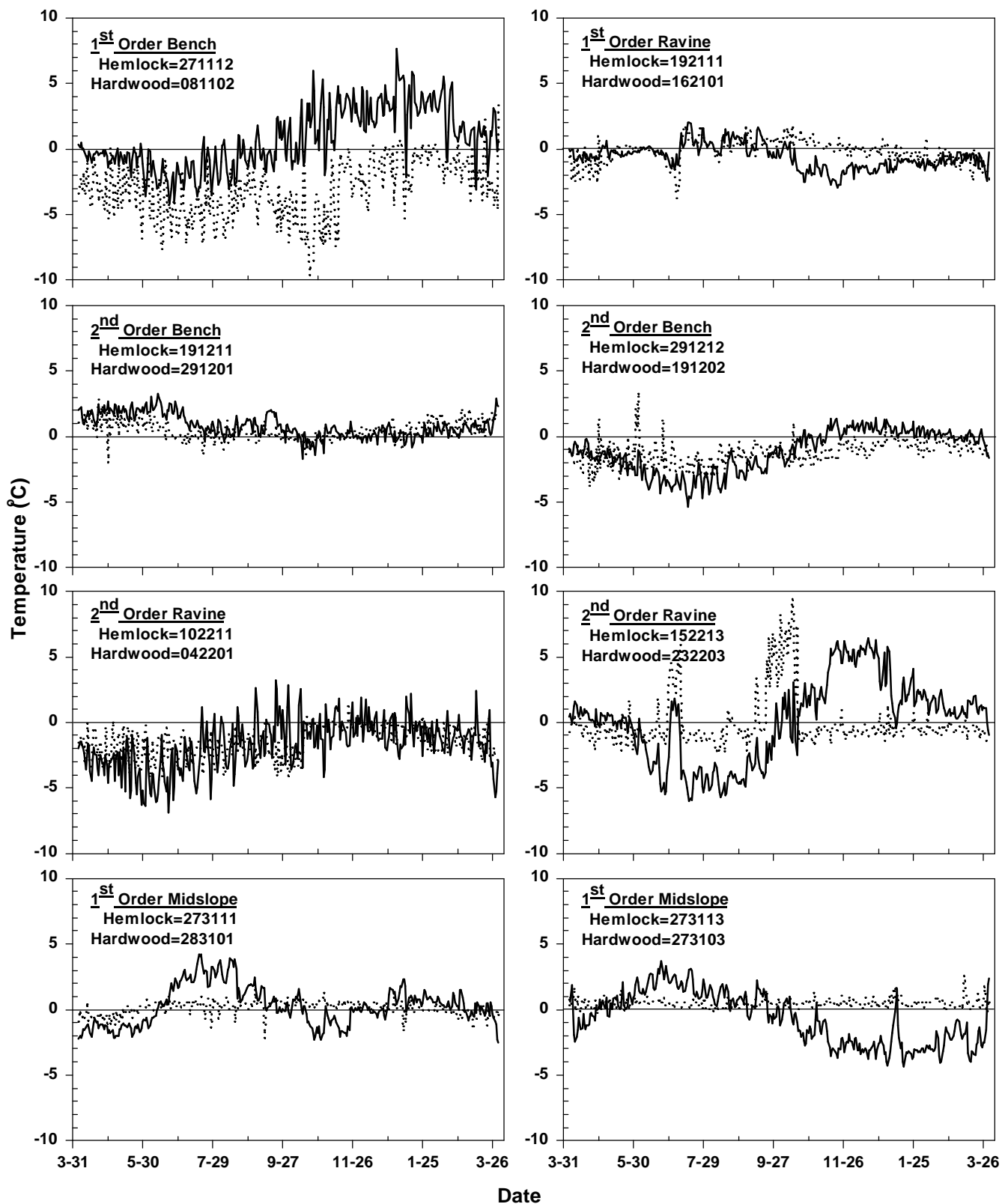


Figure 4-3. Differences in median daily temperature (solid line) and diurnal range (dashed line) between hemlock and hardwood site pairs between spring 1997 and spring 1998. Data from hardwood sites were subtracted from data from hemlock sites so values greater than 0 indicate hemlock was warmer (in the case of median line) or temperature was more variable (in the case of diurnal variation line). Stream type and site numbers are also shown.

The predominant pattern described above could have been produced in two ways. First, stream temperatures could have been different initially. That is, hemlock and hardwood forests may have had similar influences on stream temperatures but temperature patterns were different upstream, near stream sources. Second, surrounding vegetation could have influenced temperatures as water proceeded through the forest. We placed additional loggers several hundred meters upstream of study sites (Fig. 1-6) in an effort to determine changes in stream temperature patterns as water passed through the forest. Upstream-downstream differences in stream temperature suggested that indeed hemlock and hardwood forests differed in their respective influence on stream temperature. For example, during the summer, water passing through hemlock forests either cooled more or warmed less than water passing through their paired hardwood forests (Fig. 4-4). Likewise, during the winter, water tended to warm or remain relatively stable in streams draining hemlock while cooling substantially in paired hardwood forests (Fig. 4-4). In general, these patterns were consistent with the same four site-pairs described above. Again, both 1st order midslope sites showed the opposite pattern.

In addition, during the summer, streams draining hemlock tended to warm more slowly in response to warming air temperature than their hardwood counterparts (Fig. 4-5). Again, the pattern was consistent for three of the four site-pairs described above. Midslope sites again responded differently than the other stream types and no differences due to forest type were observed for the 1st order ravine site pair and one of the 2nd order bench sites (Fig. 4-5). Also, one of the two 2nd order ravine site pairs showed a different pattern where there was essentially no relationship at all between air and water temperature for much of the summer. However, we believe that this is due in large measure to ground water influence on the temperature of the stream draining the hardwood forest. Temperatures remained almost constant during much of the summer at that site. Those occasions when temperature did fluctuate (dotted line figure 4-5) suggested that water temperature responded in the same way as the other three site pairs (i.e., more dramatically in the hardwood than hemlock site) when surface water flow predominated.

Probably more important than mean, medians and other measures of central tendency to fish and invertebrates are the seasonal extremes in temperature. With the exception of mid-slope sites, summer maxima were higher in streams draining hardwood forests (Fig. 4-6). For example, summer maxima in streams draining hardwood forests exceeded 20°C over 18% of the time compared to less than 3% in streams draining hemlock. Likewise, winter minima were lower in streams draining hardwood (Fig. 4-6). Minimum temperatures dropped below freezing 8% of the time in hardwood sites compared to only 0.2% in hemlock sites. Taken together, differences in temperature patterns between forest types suggest that streams draining hemlock were less extreme and more stable.

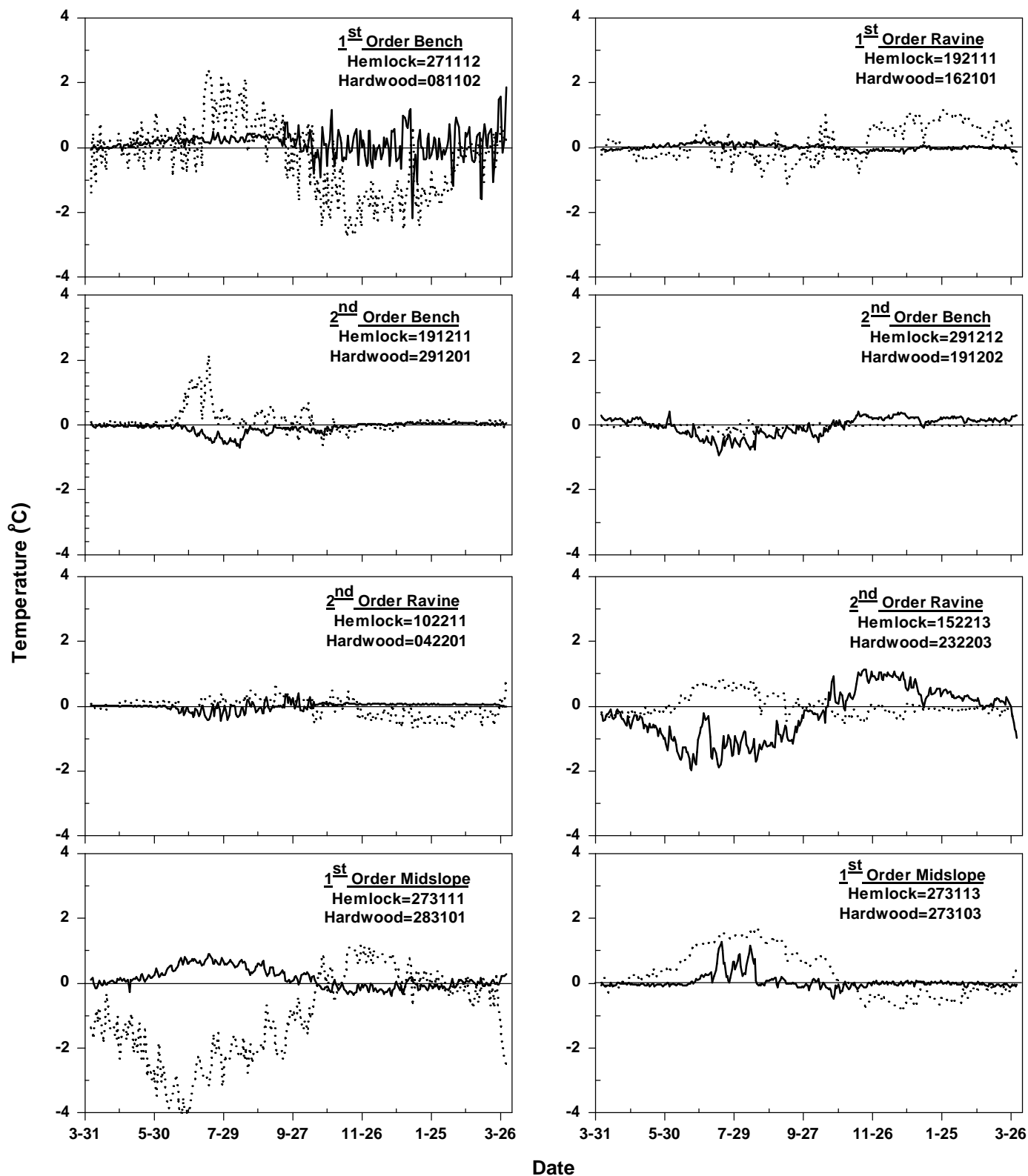


Figure 4-4. Comparisons of the effects of forest type on average stream temperature. Changes in stream temperature per 100 meters of stream was calculated as the difference in mean daily temperature between a site at the bottom of the study reach and one several hundred meters upstream. Thus, positive values indicate stream temperature warmed as water progressed downstream. Solid lines refer to stream draining hemlock and dashed lines refer to the hardwood pair. Stream type and site numbers are shown.

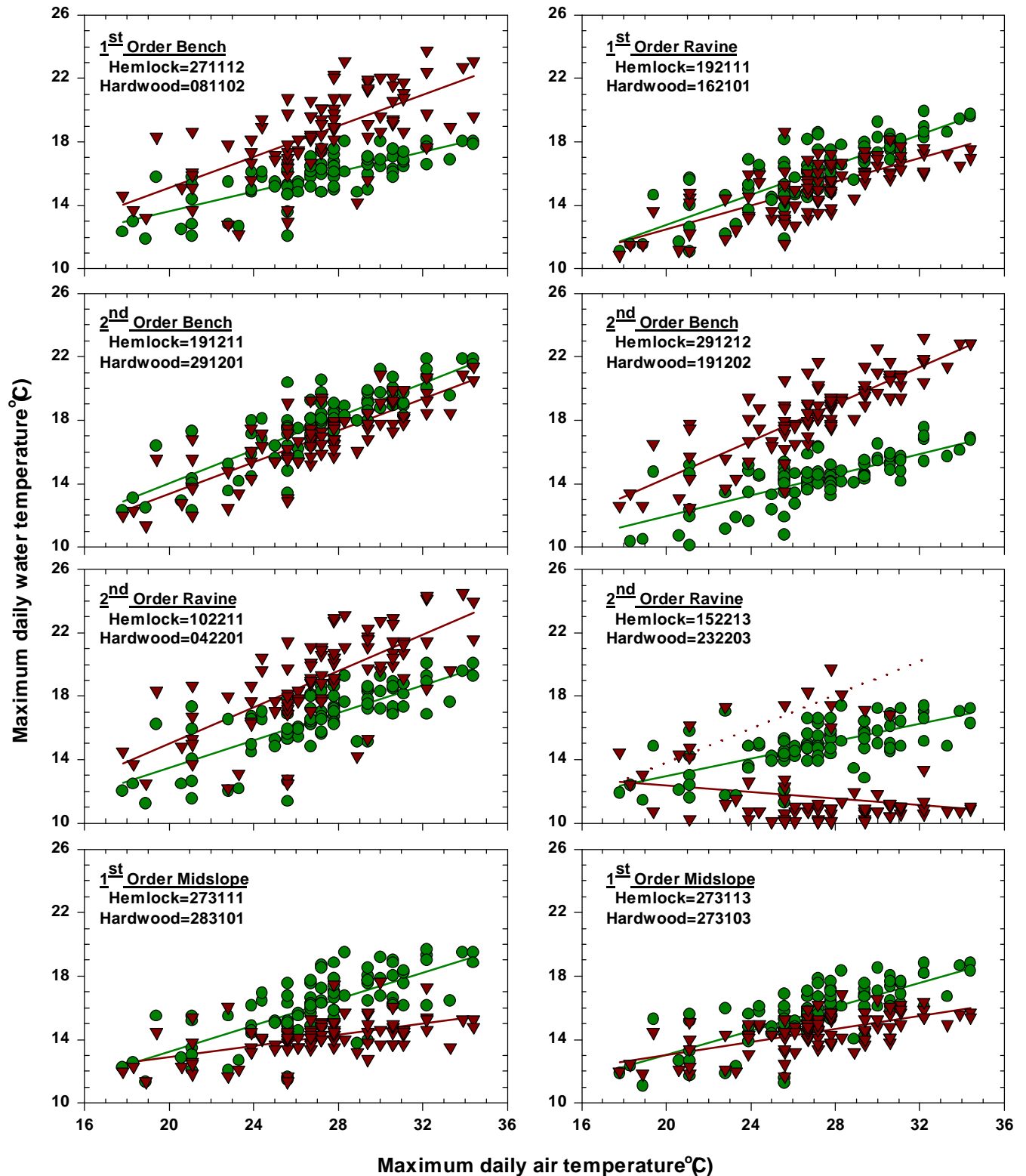


Figure 4-5. Comparison of air temperature - water temperature relationships between hemlock-hardwood site pairs. Data included observations between May and October 1997. Hemlock sites with green lines and symbols, hardwood sites with red.

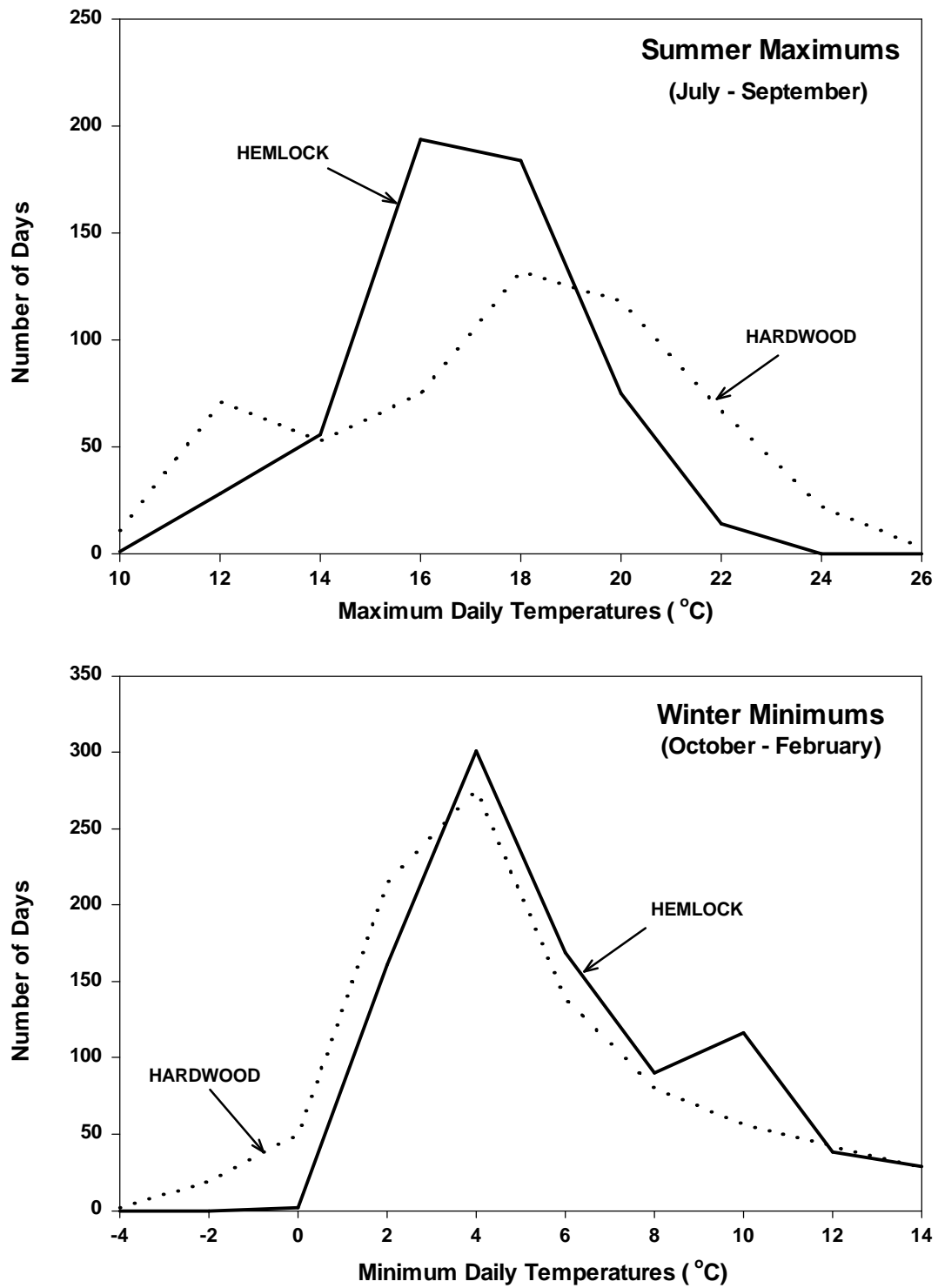


Figure 4-6. Comparison of the distributions of summer maximum temperatures (July-September) and winter minimum temperatures between streams draining hemlock and hardwood forests. Data from first order mid-slope sites were omitted because both temperature patterns and diversity patterns differed from those of the other stream types.

Hydrologic Patterns

We used flow data from the USGS gaging station on the Bushkill River to characterize rainfall patterns throughout the Park. We found stream flows to be normal (i.e., close to the long-term average) during the spring, when invertebrate sampling was conducted. However, the summer was very dry with stream flows during the months of July and August falling well below what would be considered normal for that time of year (Fig. 4-7).

The result of the dry summer in 1997 was that a substantial portion of our study streams dried up. However, streams draining hardwood forests dried significantly more than their hemlock pairs (Table 4-3; $\chi^2=9.429$, $df=3$, $p=0.024$). These patterns suggest that in particularly dry years, streams draining hardwood forests are more likely to dry, and fish and invertebrates would be unable to complete their life cycles.

Table 4-3. Extent to which DEWA study streams dried up during the summer of 1997. Extent of drying was estimated visually to the nearest 10% of the stream channel bottom between 07 July and 16 July, 1997 when fish collecting occurred. Mostly wet = >50% of stream bottom was wetted; mostly dry = <50% of stream bottom wetted. See Table 1 in Chapter 3 for more detail.

	Number of Sites (%)	
	Hemlock (N=14)	Hardwood (N=14)
Completely Dry	0 (0.0%)	4 (28.6%)
Mostly Dry	2 (14.3%)	5 (35.7%)
Mostly Wet	3 (21.4%)	0 (0.0%)
Wet	9 (64.3%)	5 (35.7%)

DISCUSSION

There are several mechanisms by which the composition of streamside vegetation can influence fish and aquatic invertebrate communities. The most direct influence would be in regulating the amount and quality of energy inputs. Headwater streams in relatively undisturbed, forested catchments are largely heterotrophic because surrounding vegetation both limits primary production through shading, and directly provides energy in the form of leaves and wood that fall into the stream (Cummins 1992). Thus, forest-specific differences in the quantity, timing, and variety of leaf litter inputs could affect the distribution and abundance of aquatic species. There is some evidence that hemlock and other conifers contribute more allochthonous inputs annually than mixed hardwood forests (Anderson and Sedell 1979, Molles 1982). On the other hand, there is also evidence that shredder invertebrates prefer hardwood leaf species and do not grow as well when fed conifer or deciduous evergreen needles (Anderson and Grafius 1975). Thus, it is unclear what the net effect of forest-specific differences in allochthonous inputs would be on aquatic biodiversity.

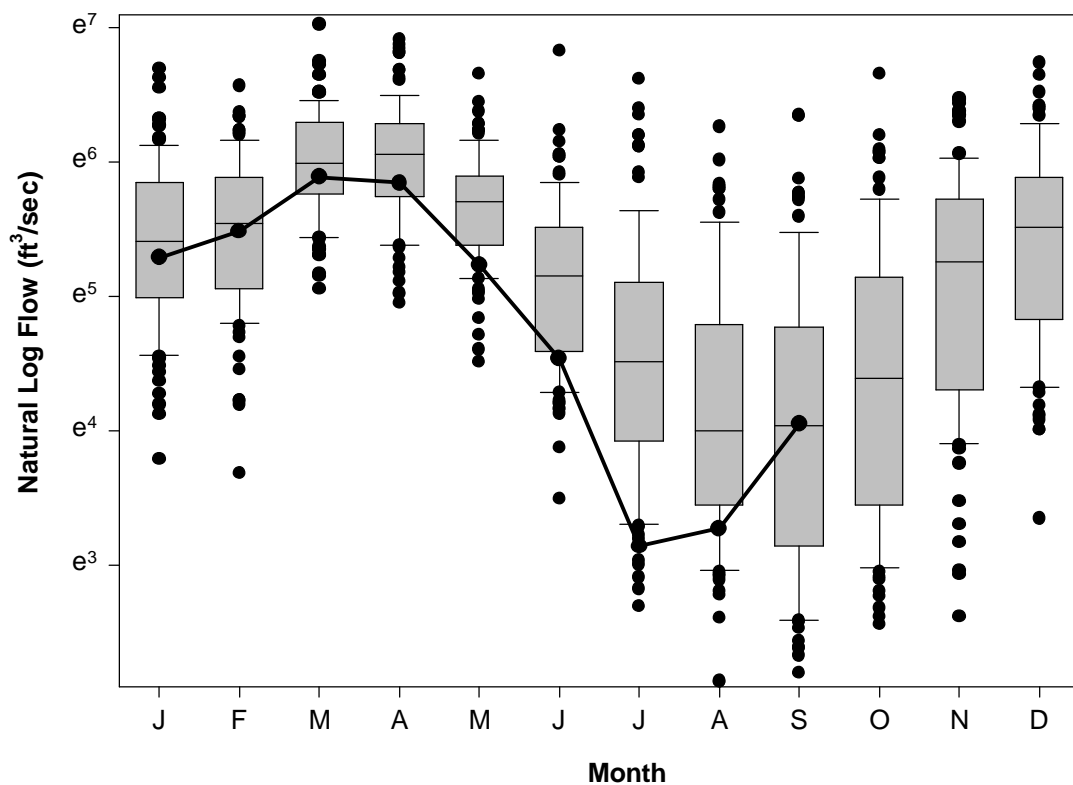


Figure 4-7. Box plots show the distribution of mean flows at the Bushkill River gaging station (#01439500) at Shoemakers, PA, for a 90 year period between 1908 and 1997. Solid lines within each box plot represents the median, the limits of the box represent 50% of the values, limits of error bars represent 90% of the values, and individual points represent the remaining data. The solid line shows median discharge for the 1997 study year. Data taken from USGS web site (<http://waterdata.usgs.gov/nwis>)

We did not measure leaf litter inputs directly. However, there is some indirect evidence that leads us to believe that differences in energy subsidies between forest types were not responsible for higher aquatic invertebrate diversity and brook trout occurrence observed in streams draining hemlock forests. First, if diversity differences were due to the presence of hemlock needles as an additional or alternative food source, we would expect the shredder-detritivore trophic group to be most affected. Shredding insects are the first macroinvertebrates to use leaf litter as food and tend to be the most selective of all the detritus feeders (Anderson and Sedell 1979). However, we found no significant differences in shredder diversity between forest types (Fig. 2-2). Secondly, if the quantity of leaf litter was higher in streams draining hemlock, we would expect higher total densities in addition to higher diversity. This was also not the case as total densities were actually significantly higher in streams draining hardwood (Fig. 2-1).

Another mechanism by which streamside vegetation can influence aquatic community structure is the role that large woody debris plays in controlling the amount and distribution of microhabitats. In addition to directly adding habitat complexity by providing additional substrate for invertebrates and cover for fish (O'Conner 1991, Richards and Host 1994), presence of large woody debris in streams creates barriers to flow and consequently facilitates the formation of dam and scour pools, thereby increasing microhabitat diversity (Swanson and Lienkaemper 1978, Gregory 1992). In addition, large woody debris increases retention time of organic matter and nutrients required by aquatic species (Bilby 1981, Harmon et al. 1986). Moreover, there is evidence that hemlock forests contribute substantially more woody debris to streams they drain than corresponding mixed hardwood forests (Anderson and Sedell 1979), and that conifer wood decays much more slowly than hardwoods (Harmon et al., 1986). Therefore, streams draining hemlock may be expected to have a more complex habitat structure that could directly and/or indirectly influence both fish and invertebrate diversity and abundance.

In DEWA, streams draining hemlock had significantly higher microhabitat diversity overall than their hardwood counterparts, and this pattern was consistent for most stream types (Fig. 4-2). However, we observed no differences in the amount and size distribution of LWD between streams draining hemlock and mixed hardwood forests. Thus, other factors besides differences in large woody debris inputs between forest types could have been responsible for higher stream habitat diversity in hemlock-dominated watersheds. Although we tried to account for variation in terrain in our study design, it could be that relatively subtle differences in topography could have profound differences on the distribution and abundance of microhabitats. However, residence time for woody debris in streams is highly variable (Gregory 1992) and the influence of large woody debris on the processes that control channel morphology and microhabitat diversity are long-term. Thus, it could also be that higher microhabitat diversity observed at hemlock sites was created by higher large woody debris inputs in years past or the cumulative inputs over a long period of time. Although the relationship between microhabitat diversity and aquatic macroinvertebrate diversity was not entirely consistent (i.e., site pairs where the hemlock stream had significantly more microhabitat types were not always the same site pairs where invertebrate diversity was higher in the hemlock site and visa versa) these data suggest hemlock effects on microhabitat diversity could have been partially responsible for the observed community structure differences.

Upland and riparian vegetation also have a profound influence on instream nutrient dynamics (e.g., Pinay et al. 1990). For example, in a study comparing nutrient processing rates between hemlock and sugar maple (*Acer saccharum*) forests, Mladenoff (1987) found nitrogen mineralization rates (i.e., proportion of available nitrogen used) to be higher in hemlock suggesting hemlock forests are more efficient in removing nitrogen from soils. Consequently, nitrogen concentrations in streams draining hemlock forests may be expected to be lower than in streams draining hardwood forests. Furthermore, nitrogen processing rates have been shown to increase dramatically with hemlock woolly adelgid-induced hemlock mortality (Jenkins 1998).

In turn, nutrient loads can affect aquatic communities by increasing primary and secondary productivity (e.g., Hall et al. 1970) and by depleting oxygen levels (Wetzel 1983). Although no differences in phosphates, ammonia, and nitrates were observed between forest types, total nitrites were significantly lower in streams draining hemlock (Fig. 4-1). However, we believe it is unlikely that differences in nitrite levels had a significant effect on aquatic community structure at our study sites. Light is probably at least as important in limiting primary production as nutrients in these low-order streams, and oxygen levels are near saturation throughout the year due to the continuous mixing associated with turbulent flow patterns in high gradient watersheds.

Finally, streamside vegetation exerts considerable control on stream temperature and flow patterns. For example, in the extreme, forest removal increases stream temperatures (Swift and Messer 1971) and results in more extreme (i.e., higher highs and lower lows) flow patterns (Graf 1980). We were unable to find any published information that compared the relative effects of hemlock and other forest types on thermal and hydrologic patterns. Nevertheless, hemlock forests may be expected to provide more shading annually than mixed hardwood forests. This may provide a blanket effect, where cumulative temperature and moisture levels remain more stable.

Low order, high gradient streams such as those sampled in this study, are generally believed to be disturbance-controlled. That is, the diversity and structure of aquatic communities are influenced more by the frequency and magnitude of floods, droughts, and temperature extremes than by more deterministic factors such as predation and competition (Resh et al. 1988, Grossman et al., 1990). Thus, factors that enhance environmental stability would be expected to have positive effects on the diversity of aquatic communities. Empirical studies with invertebrates (e.g., Death and Winterbourn 1995) and fish (Grossman et al. 1982) support this general hypothesis.

We found some evidence that hemlock forests had a significant buffering effect on thermal patterns. In general, stream temperatures at hemlock sites were less sensitive to changes in air temperature (Fig. 4-5) resulting in cooler summer temperatures and warmer winter temperatures (Fig. 4-3). Furthermore, summer and winter extremes in temperature were more moderate in streams draining hemlock (Fig. 4-6). This buffering effect could have positive effects on both invertebrates and fish, but may be particularly important in explaining higher brook trout occurrence and abundance patterns in streams draining hemlock. Specifically, brook trout prefer stream temperatures of 14-16°C and spawning is virtually restricted to water of 15°C and below. Furthermore, the upper lethal limit of hatchlings is 20°C, and adults are rarely found in streams

where summer temperatures exceed 21°C (Jenkins and Burkhead 1993). The fact that summer maxima exceeded 20°C over 17% of the time in streams draining hardwood forests compared with 3% of the time in streams draining hemlock (Fig. 4-6) strongly supports the conclusion that a hemlock-induced effect on moderating stream temperatures was responsible for the distribution and occurrence patterns of brook trout that we found.

There was also evidence that the extent to which streams dried up was influenced by forest type. Fewer of the streams draining hemlock forests dried up (Table 4-3), possibly owing to the temperature differences described above. Although 1997 represented a particularly dry summer (Fig. 4-7), organisms at DEWA can expect to be subjected to conditions as dry or drier every 11 years (recurrence interval calculated from gaging station data in figure 4-7 using Weibull probability method as described in Gordon et al., 1992). Clearly, during such dry years, a large fraction of both fish and invertebrates will fail to survive and reproduce. Consequently, their occurrence and abundance at sites that frequently dry will be largely determined by re-colonization potentials. In contrast, streams that maintain sufficient flows during dry years will most certainly support more species.

In summary, no single habitat variable directly correlated with aquatic invertebrate diversity or brook trout occurrence differences observed between forest types (Chapters 2 and 3). However, we found forest type had a significant, concomitant influence on several habitat variables, each of which could have contributed to some extent, to the observed differences in aquatic community structure. Although hemlock effects on microhabitat diversity and nutrient concentrations may have contributed to aquatic community differences observed between forest types, we believe that hemlock mediated increases in thermal and hydrologic stability were most important in explaining higher invertebrate diversity and brook trout occurrence patterns.

From a broader perspective, the observed hemlock effects on stream conditions may have an influence in other parts of the drainage basin. For example, although higher nitrite concentrations in streams draining hardwood forests are likely to have a minimal effect on biological communities in these small, high gradient streams, the cumulative effect on the Delaware River and ultimately the Delaware Bay could be significant if hemlock forests throughout the basin die and become replaced by hardwood. Nutrient levels in the Delaware River are of particular concern and specific nutrient limits have been established (Delaware River Basin Commission Water Quality Regulations 1996). If hemlock forests within DEWA succumb to HWA and are replaced, as expected, by mixed hardwoods, then nitrite levels may be expected to increase in the Delaware River. Such increases could increase primary production and decrease dissolved oxygen levels in the River and the Bay. Likewise, hemlock-mediated increases in thermal and hydrologic stability may also cascade to other portions of the basin. Survival and productivity of Delaware river fishes, particularly trout and shad, may be limited by the relative severity of summer, base-flow conditions. Stable discharges of cooler water from hemlock-dominated watersheds may provide refugia during these summer extremes.

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